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HISTOGENESIS OF THE INFLORESCENCE AND FLOWER OF *TRITICUM AESTIVUM* L.

By C. Barnard*

[*Manuscript received September* 13, 1954]

Summary

In *Triticum* the apical meristem of the spike and spikelets is similar to that of the vegetative axis: a two-layered tunica encloses a central corpus. Leaf primordia arise by the periclinal division of cells of the tunica, the corpus contributing nothing to their development. Spikelet primordia are initiated in periclinal divisions of cells of the outer layer of the corpus (sub-hypodermis). Their mode of origin is comparable with that of vegetative buds.

The glumes and lemmas arise in the same manner as the foliage leaf; the flower primordia by divisions in the sub-hypodermis like the spikelets. The early histogenesis of the palea, lodicules, and carpel is also essentially the same as that of the foliage leaf, whilst the stamens arise as cauline structures like the spikelets and flower primordia.

The ovule is derived directly from the apex of the flower primordium and the integuments originate in the manner of foliar structures.

The significance of these observations in the interpretation of the floral morphology of *Triticum* is discussed.

I. Introduction

Contributions in histology to the interpretation of floral morphology have been mainly in the field of comparative and developmental vascular anatomy. Few studies have been made of the histogenesis of floral organs and these have been concerned only with dicotyledonous plants.

Joshi (1947) has competently reviewed the literature on the histogenesis of the flower and has discussed at length the conclusions of workers in this field regarding the morphological nature of the flower and its various parts. The position very briefly is as follows. Gregoire (1938), on the basis of a comparison of the histogenesis of the flower and organs of the vegetative axis in a number of genera, concluded that the classical morphological concept of the homology of petals, stamens, and carpels with the foliage leaf was in error and that all parts of the flower, except the sepals, were without homology among organs of the vegetative axis. Brooks (1940), from a study of the vegetative and floral apices of *Amygdalus communis* L., supported Gregoire's contention. Satina and Blakeslee (1941, 1943) on the other hand, working with periclinal chimeras of *Datura stramonium* L., found no essential differences between the histogenesis of the apical meristem in leaf and flower buds; that the histogenesis of the sepals and petals was similar to that of the foliage leaf; and that the stamens and carpels arose as axial structures. McCoy (1940), investigating *Frasera carolinensis* Walt., Engard (1944), working with *Rubus* spp., and Boke (1947, 1949), studying *Vinca rosea* L., observed that foliage leaves and all floral appendages arose in the same manner and therefore subscribed entirely to the classical concept. Finally, Tepfer (1953) examined and compared histogenesis of the vegetative and floral apices and their appendages in *Aquilegia* and *Ranunculus*.

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These two genera were among those examined by Gregoire. Tepfer found the initiation and early ontogeny of all appendages very similar, their origin being in the inner layer of the tunica and the outer layer of the corpus of the axis.

It is apparent that considerable differences may exist in some plants between the organogenesis of vegetative and floral buds whilst in others it appears comparable. The differences which have been so strongly emphasized by Gregoire, however, were shown by Joshi (1947) and Tepfer (1953) to be not so absolute or irreducible as Gregoire claimed. Further, the fact that differences do occur does not invalidate conclusions of homology when ontogeny is similar. Joshi's (1947) opinion therefore, that the classical concept of the nature of the flower, with a few minor modifications, is supported by histogenetic studies, seems justified. Representatives of many more groups of flowering plants need to be examined before the facts revealed by histogenetic study may be more confidently and specifically interpreted.

No account has been published of the histogenesis of the inflorescence and flowers of *Triticum aestivum* L., nor of any other member of the Gramineae. The histology of the vegetative growing point and the initiation of the leaf and axillary bud, however, have been examined in *Triticum* by Rösler (1930), in *Avena* by Kliem (1937), and in *Agropyron* by Sharman (1945). The study here presented of the histology of organogenesis in the floral region of *T. aestivum* compared with the accounts of Rösler, Kliem, and Sharman will clearly show the homologies between vegetative and reproductive structures in the Gramineae.

The histological data are preceded by a brief account of the morphogenesis of the spike, although this has been described previously by many workers, including Percival (1921) and Bonnett (1936). Such an account is necessary here to enable the reader to follow easily the histogenesis of the organs concerned and to correct in some respects the previous descriptions.

II. Methods and Materials

This investigation was made as a prelude to the study of the morphogenesis and histogenesis of the spikelet in certain basal sterile speltoid mutants of *T. aestivum* (*Triticum vulgare* Host.) which were discovered and described by Frankel and Fraser (1948). No essential differences were found between the histogenesis of these speltoid mutants and typical *aestivum* varieties except in the development of the lower flowers of the spikelet. For all other phases of development the speltoid types have therefore been used as well as standard varieties of *T. aestivum* in this study. The differences in the mutants will be described in a separate communication.

Two standard varieties of *T. aestivum*, viz. Victor and Yeoman, together with the speltoid mutants St_1, St_2, and St_f, were used; supplementary observations were made on the variety Federation.

St_2 and Federation are spring wheats in that they do not require vernalization; the others are winter varieties and need vernalization for early development of the inflorescence. All varieties except Federation were sown during the autumn of 1952 in large iron containers and in pots, and grown in the open at Canberra. Federation and St_2 were grown in a glass-house and a number of sowings was made.

Samples were taken at suitable intervals from several weeks after germination until anthesis. The developing inflorescence, with the youngest enfolding leaves and a few millimetres of the vegetative axis, was cut from the sample and fixed in formalin-acetic-alcohol. Material for the preparation of serial sections was dissected under a stereo-microscope and correct orientation for cutting was achieved by affixing the specimen to small pieces of card by means of melted agar. The agar, hardened in absolute alcohol, held the specimen securely in position and did not interfere with subsequent infiltration and embedding in wax. Orientation was also obtained by passing a fine pin through the base of the specimen. This portion of the material was pared off the paraffin block just before cutting. Sections were cut at 5 and 7 μ and stained in iron alum haematoxylin and erythrosin. Safranin and tannic acid were also used but were not so satisfactory.

For the study of morphogenesis, specimens were stained in acid fuchsin in 95 per cent. alcohol. They were then dissected in absolute alcohol under a stereomicroscope, using when necessary a Singer micro-dissector. Dissections so made may be fixed to cards by melted agar and kept indefinitely in alcohol.

Drawings were made by photographing the subject and tracing a projected image from the negative. Minor adjustments of features observable only by refocusing the microscope were then introduced. In some cases, adjustments have been made after reference to adjacent sections of the series. This has been necessary because of the great difficulty of obtaining single sections which show all the features it is desired to illustrate in absolute median view.

III. Morphogenesis

(a) *The Spike*

The transition from the vegetative to the reproductive stage of growth commences when there are from five to seven expanded or externally visible leaves on the main axis and its growing point is just about at ground level or no more than 1 cm above it.

The first morphological indication of spike formation is a rapid elongation of the apical dome (Plate 1, Fig. 1). The apex of the axis prior to this time has been a blunt, short cone; it now becomes an elongated cone. Leaf initials are formed rapidly and in close succession, but the further development of these primordia progressively diminishes (Plate 1, Fig. 2). The "cone" thus becomes more elongated.

In winter varieties the commencement of this change in the behaviour of the apical meristem of the main axis was coincident with the formation of the 13th or 14th plastochron. For whilst there are six or seven visible leaves in these types at this stage, there are also present six or seven younger leaf primordia in various stages of development. The 10th leaf is a primordium just large enough to overtop the dome-shaped apex and form a "cowl" around it, whilst the 14th leaf is merely a crescent-shaped ridge of tissue on one side of the apex (Plate 1, Fig. 1 (*lp*)). In St_2 and Federation, the spring varieties, only five leaves were visible and the formation of the 10th or 11th plastochron was the beginning of the transition to the reproductive phase. This stage is reached under field conditions about 10 weeks

after sowing in autumn; under glass-house conditions it may be reached in Federation in less than 1 month, and in St_2 in approx. 6 weeks from sowing. Spike initiation in tillers takes place later and when not so many leaves have been formed on the tiller.

The elongation of the apical dome and the rapid formation of leaf initials continues until a stage is reached when between the "cowl" and the apical meristem there may be 16 or more leaf initials, the youngest eight or nine being no more than crescentic ridges around the axis (Plate 1, Fig. 3). Small bulges then appear in the axils of the 13th or 14th leaf primordium (the 11th or 12th in St_2), the bases of which completely encircle the axis. As the apex continues to elongate axillary primordia form in rapid acropetal succession in the axils of the upper leaf initials. This results in a "double ridge or ring" appearance (Plate 1, Figs. 4 and 5). The axillary primordia (*sp*) develop into spikelets.

The subtending leaf primordia are more prominent towards the base of the developing spike. For a short period only are the subtending leaf primordia clearly visible together with the spikelet primordia in the upper portion, as the rapid growth of the spikelet primordia soon obscures a view of the subtending leaf initials. The subtending leaf initials of the lower spikelets are still apparent when the spikelet primordia are quite large (Plate 1, Fig. 6).

The apex of the vegetative axis, which has now become the apex of the young spike, becomes the primordium of the terminal spikelet (Plate 1, Fig. 7).

In the axils of the lowermost foliage leaves, buds develop which grow into tiller shoots; in the axils of the upper foliage leaves buds are formed but fail to develop into shoots; in the axils of the leaf primordia immediately below the young spike no axillary structures are formed. The initiation of axillary structures in the higher leaf primordia results in spikelet formation.

The transition from the formation of vegetative to reproductive structures may therefore be stated as follows:

Leaf initials are formed more rapidly on the vegetative axis, but progressively fail to develop. When the "inhibition" of leaf primordia growth reaches a certain stage, axillary bud differentiation commences. Following a short transition period the growth of the foliar primordia completely ceases and growth of the axillary bud initials becomes dominant. There is no information as to when this change from vegetative growth to the production of reproductive structures becomes irreversible. Elongation of the internodes of the vegetative axis commences when the spike starts to form.

(*b*) *The Spikelet*

The primordium of the apical spikelet normally develops more rapidly than any other. The lateral spikelets just above the centre of the spike are usually slightly more advanced than those above and below, and the basal spikelets the most backward in growth (Plate 1, Figs. 7 and 8). Whilst this is the usual pattern, considerable variation occurs in the relative rates of development of the spikelets. Occasionally the most distal spikelets are the most advanced, and development is progressively and markedly more backward in the lower spikelets (Plate 1, Fig. 5);

occasionally also development in the apical spikelet is markedly behind that of the most advanced lateral spikelets (Plate 1, Fig. 6).

The first and second glume (*gl*) and the first and second lemma (*l*) differentiate successively as alternate lateral ridges which more than half encircle the spikelet axis. They may be seen in the spikelets of the spikes depicted in Plate 1, Figures 8 and 9. They show particularly clearly in the terminal spikelet of Plate 1, Figure 8. As the primordium of the third lemma is forming, a flower primordium becomes visible in the axil of the first lemma as a rounded protuberance (Plate 1, Fig. 10). The young spike at this stage is 2-3 mm long.

The apex of the spikelet continues to grow forward and generally forms 10 lemmas, each of which subtends an axillary structure which is destined to become a flower primordium. Occasionally, and particularly under glass-house conditions of high temperature and humidity, spikelets may differentiate many more flowers.

(*c*) *The Flower*

The flower primordium before differentiation of its parts is an elongated hemispherical structure. The formation of a narrow ridge of tissue along its posterior side initiates the palea. This is followed by the appearance of four "papillae", which represent the rudiments of the stamens and carpel. The papillae of the two lateral stamens usually arise first, followed by those of the anterior stamen and carpel. Whilst the rudiments of the lateral stamens are hemispherical, that of the anterior one is frequently flattened in an antero-posterior direction. The papilla of the carpel rudiment is actually a horseshoe-shaped ridge of tissue encircling the apex of the flower axis. It develops at first most rapidly on the anterior side of the apex; then development accelerates on the posterior side with the result that the apex of the flower primordium becomes completely enclosed. The lodicules are the last of the floral organs to become clearly visible.

In Plate 1, Figure 11, flower primordia in which stamens (*s*) and carpel (*c*) are present as large papillae are illustrated. The palea (*p*), which grows at first most rapidly on its lateral edges, may be seen projecting from the posterior side of the primordium. In Plate 1, Figure 12, an anterior view of a young flower primordium at about the same stage of development as that shown in Plate 1, Figure 11, is depicted. It shows the lodicules at first represented by a very narrow ridge of tissue (*r*) along the whole of the anterior side of the flower primordium. The growth of the centre of the palea soon overtakes that of its lateral wings as shown in Plate 1, Figure 13, which gives a posterior view of a slightly older flower primordium. In this photograph, it will be observed that the palea (*p*) is only about half the height of the stamens when they have developed quadrilocular anthers. Growth of the palea then accelerates and soon it overtops the stamens. In Plate 1, Figure 14, an older flower primordium shows the rapidly developing palea, the two lodicules, and three stamens. The lodicules have originated as outgrowths of the anterior ridge of tissue noted above. The anterior stamen is somewhat smaller than the two lateral stamens and the carpel is obscured.

The apex of the flower primordium develops directly into the ovule; this will be made clear in the accounts of its histogenesis.

Later developments in the morphology of the flower are well known and do not need to be described here.

IV. Histogenesis

(a) *Apex of Spike*

The apex of the vegetative axis, when it commences to elongate in the first stage of inflorescence formation, has a two-layered tunica surrounding a central corpus. Because, however, both layers of the tunica and the cells of the outer layer of the corpus each play a distinctive part in histogenesis, the author prefers to use the terms adopted by Sharman (1945) in his description of the vegetative apex of *Agropyron repens* (L.) Beauv.

The tissues of the apex are very clearly defined in three zones (Plate 2, Fig. 1). There is a single outer layer of cells which Sharman terms the dermatogen. Cells of this layer divide by anticlinal walls only, except where a leaf primordium is initiated. Within the dermatogen is another single layer of cells—the hypodermis. The cells of this layer are generally longer radially and tangentially than they are vertically. Division of cells in the hypodermis is also by anticlinal walls only, except where leaf primordia are formed. Within these two "shells", which constitute the tunica, there is a central core of cells or corpus. Cells of the corpus differ from those of the hypodermis in that their nuclei are smaller compared with their volume and their cytoplasm becomes vacuolated much earlier and stains less densely. These features are illustrated in Plate 2, Figures 1 and 2, which represent longitudinal sections of apices comparable with those shown in Plate 1, Figures 1 and 2, respectively.

Both the dermatogen and hypodermis arise in the first place by the division of apical cells, that of the hypodermis being immediately below that of the dermatogen. There is some evidence that the cells of the central core may also originate in the division of a single apical cell. This point, however, is not clear; usually there seems to be a small group of dividing cells at the apex of the core and no single cell of this group may be designated the apical one. Divisions within this small group of cells take place in all directions. The outer cells of the core are sometimes vaguely defined as a layer somewhat different from the inner cells. Division in this layer is concerned with the origin of axillary structures and the layer is therefore conveniently given a separate name—the sub-hypodermis.

(b) *Origin of Leaf Primordia*

Leaf primordia are formed entirely from the dermatogen and hypodermis. The process is illustrated in Figure 1. The periclinal division of one or two cells of the hypodermis is the first indication of leaf formation and these divisions take place close to the apex. A single cell of the dermatogen immediately adjacent then divides periclinally and further periclinal divisions occur in the cells of the hypodermis and dermatogen in the same horizontal plane over the whole area of leaf insertion. Hypodermal cells above and below those which have already divided undergo radial mitosis until a vertical tier of four or five divided hypodermal cells is formed. The area of leaf initiation thus becomes a zone four or five hypodermal

cells high, extending transversely around the axis. In the lower leaf primordia this zone ultimately encircles the axis completely. The 13th or 14th leaf primordium, which subtends the lowest spikelet in the winter wheats, may just completely encircle the axis. The leaf primordia which subtend the upper spikelets do not, however, develop far enough for complete encirclement to occur. As the leaf initials towards the apex of the spike fail to develop beyond the early stages of differentiation, so do they become more restricted to the central point of insertion. The general features of leaf development on the elongated axis are shown in Plate 2, Figures 2 and 3.

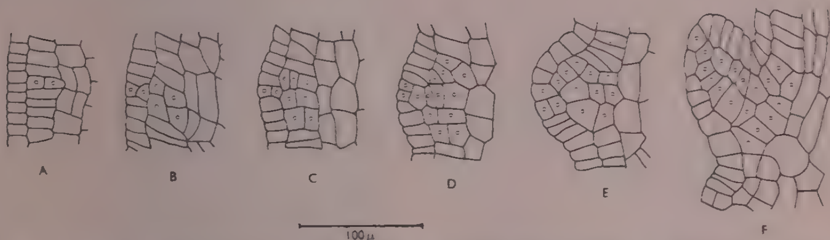

Fig. 1.—Origin of foliar primordium shown in longitudinal section. *A* shows periclinal division of hypodermal cell. *B*, *C*, *D*, and *E* show periclinal division of dermatogen cell and division of further hypodermal cells. In *F*, periclinal divisions in dermatogen and hypodermal cells at base are part of the encircling sheath of the leaf below.

Subsequent development of the leaf primordium is by further periclinal division of the derivatives of the original hypodermal and dermatogen cells. A periclinal division may take place in several cells of the sub-hypodermis immediately below the active hypodermal cells. Only one division occurs and no derivative cells contribute to the tissue of the leaf primordium. It is therefore correct to state that the corpus contributes nothing to the formation of the leaf.

(c) *Origin of Spikelet Primordia*

The first stage in the formation of a spikelet primordium is the periclinal division of cells in the sub-hypodermis between two leaf primordia. Usually three cells in the vertical plane are concerned and after division these cells present a characteristic appearance in median longitudinal sections. Development is illustrated in Figure 2 and Plate 2, Figure 4. The direction of division of the central cell is parallel to the length of the axis, i.e. it is strictly periclinal. The plane of division of the other two cells is at a slight angle to this direction. The derivatives of these three cells undergo further division in the same planes and a slight bulge becomes apparent on the surface of the axis. At the same time a fourth sub-hypodermal cell situated immediately above the three original ones, as well as several hypodermal cells on the upper periphery of the area of initiation, divide by inclined walls. Very occasionally a periclinal division occurs in several hypodermal cells: all other divisions in the hypodermal layer are anticlinal and in the dermatogen are invariably only anticlinal. The plane of division of cells originating the spikelet primordium is therefore in the form of an arc periclinal at sub-hypodermal depth, curving to

the outside and anticlinal at the dermatogen. This merismatic activity extends transversely around half the circumference of the axis. The bulge referred to above is thus actually a narrow horizontal ridge, as seen in Plate 1, Figure 4.

Continued division of the sub-hypodermal cells, which is most rapid in the derivatives of the original two central ones, results in further protrusion of the young primordium, until it becomes a hemispherical dome-shaped structure (Plate 3, Fig. 1). At this stage it is composed of a number of regularly disposed files of cells. Usually eight rows of cells may be observed in vertical section: one row of dermatogen and one row of hypodermis on the upper and lower edges and four central rows which have been derived from sub-hypodermal cells. Merismatic activity gradually becomes restricted to the distal region which assumes the characters of a growing point.

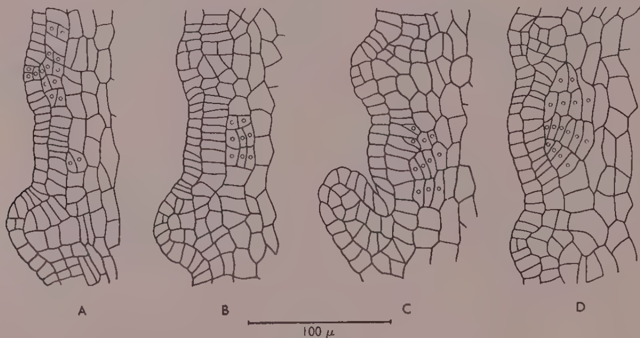

Fig. 2.—Longitudinal section of spike showing origin of spikelet primordium. The first periclinal division in the outer layer of the sub-hypodermis is shown in *A*; two periclinal divisions in three sub-hypodermal cells in *B*; inclined walls in hypodermal cells in *C*; and in *D*, the primordium is a noticeable bulge with files of cells derived from the original three sub-hypodermal cells and the first division of the fourth sub-hypodermal cell.

The leaf initials subtending the young spikelet primordia are progressively less developed towards the apex of the spike, as noted in the observations on external morphology. The subtending leaf initials of the upper spikelet primordia may be represented by only a single division of dermatogen and hypodermal cells (Plate 3, Fig. 1).

(*d*) *Differentiation in the Spikelet*

The apical meristem of the spikelet is organized in the same manner as that of the vegetative apex. It is clearly defined into the three zones of dermatogen, hypodermis, and core, although the cells of the core do not become vacuolated so early as in the vegetative apex. Each layer, including the sub-hypodermis, is characterized by distinctive histogenetical behaviour. The apical meristem of the spikelet is illustrated in Plate 4, Figure 1, and also shown in Figures 3, 4, and 5.

From the axis of the spikelet, two empty glumes and a number of lemmas are formed in acropetal succession. A flower primordium arises in the axil of each lemma.

Figure 3 depicts a longitudinal section of an apical spikelet with the primordia of two empty glumes and two lemmas. Plate 3, Figure 2, represents a longitudinal section of an apical spikelet a little further advanced in which a flower primordium is developed in the axil of the first lemma and the third lemma has just arisen. This spikelet is at the same stage as those shown in Plate 1, Figure 10.

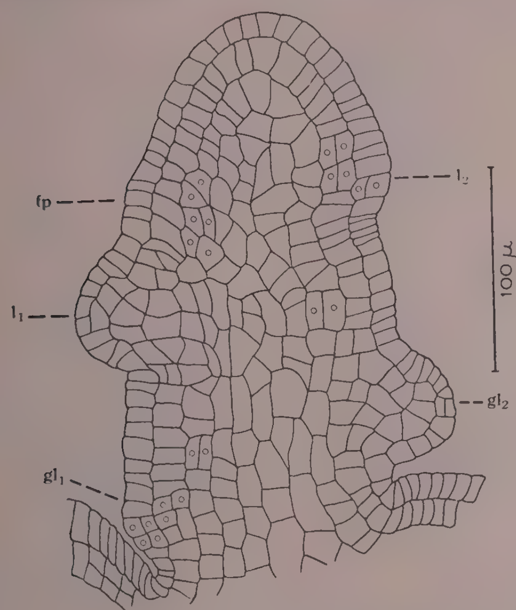

Fig. 3.—Longitudinal section of young apical spikelet. Two empty glumes (gl_1 and gl_2) and first and second lemma (l_1 and l_2) are developing; origin of first flower primordium shown at *fp*.

The glumes and lemmas develop from the axis of the spikelet in almost exactly the same way as the leaf primordia do from the axis of the spike. They are derived entirely from the dermatogen and hypodermis. The periclinal division of hypodermal cells generally precedes that of dermatogen cells. Usually three hypodermal cells and two dermatogen cells in the vertical plane divide. Occasionally, however, three dermatogen cells undergo periclinal division. In the leaf initial, it will be recalled, usually only one dermatogen cell divided periclinally and rarely two. These divisions most commonly commence near the centre of the point of insertion of the future glume or lemma; comparable divisions occur in rapid succession transversely to about half-way around the axis of the spikelet. A periclinal division of several sub-hypodermal cells may occur. These cells do not divide again for some time so that the sub-hypodermis contributes nothing to the tissue of the lemma. Illustrations of the origin of the lemma are seen in Figures 3, 4, and 5 and Plate 3, Figure 5. Subsequent development is by the division of the derivatives

of the original dermatogen and hypodermal cells. Repeated division of the dermatogen cells gives the appearance of apical growth. Later merismatic activity becomes confined to a zone near the base of the lemma.

The apical spikelet develops directly from the apex of the spike, i.e. the apex of the spike becomes the apex of the apical spikelet. The first empty glume is developed on the opposite side of the axis to the leaf initial, which subtends the

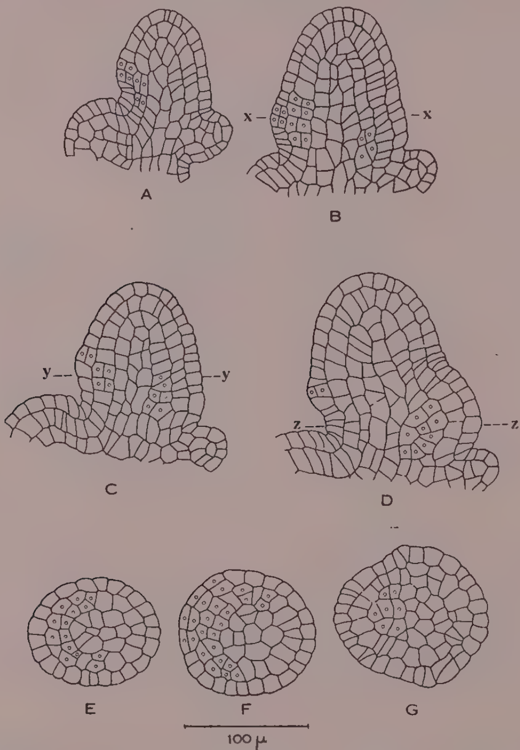

Fig. 4.—Longitudinal and transverse sections of apices of spikelets showing origin of lemma and flower primordium. *A*, from spike St_2, 15 mm long, ninth lemma arising; *B*, from spike St_f, 5.5 mm long, fifth lemma arising; *C*, from spike Yeoman, 45 mm long, eighth lemma arising; *D*, from spike 6 mm long, seventh lemma arising; *E*, transverse section in plane *y-y* of apex comparable with *C*; *F*, transverse section in plane *x-x* of apex comparable with *B*; *G*, transverse section in plane *z-z* of tip comparable with D.

uppermost lateral spikelet, and in the precise position where a further leaf initial might be expected. The first and second glumes as well as the succeeding lemmas of the apical spikelet are therefore strictly positionally comparable with the leaf initials which subtend the lateral spikelets.

Figure 4 and Plate 4, Figure 1, illustrate the differentiation and early development of the flower primordium. The flower primordia arise in essentially the same manner as the spikelet primordia and are axillary cauline structures. The first indication of flower initiation is the periclinal division of three cells in the sub-

hypodermis immediately above the last-formed lemma primordium. Inclined divisions may occur in the hypodermal cells on the upper and lateral peripheries of the future flower primordium and a periclinal division sometimes occurs on the

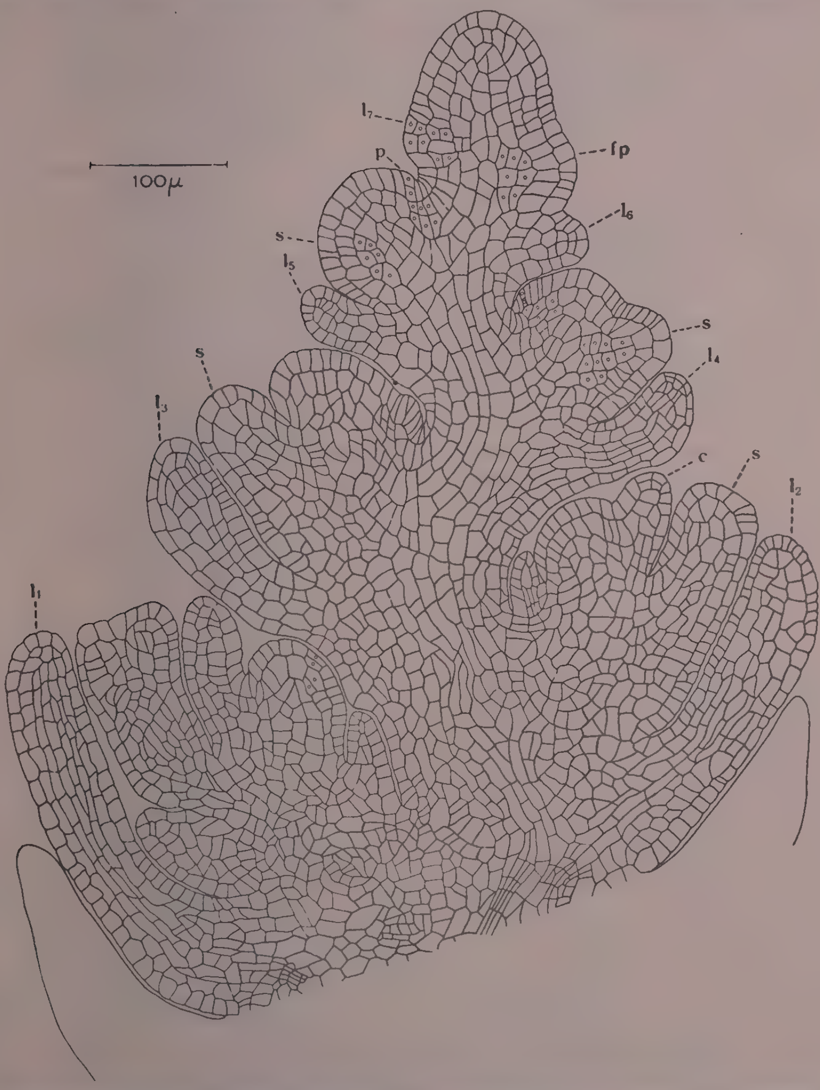

Fig. 5.—Longitudinal section of spikelet in which the seventh lemma (l_7) is arising; the origin of the youngest flower primordium is shown at *fp*. Spikelet from spike 6 mm long. *p*, palea; *s*, anterior stamen; *c*, carpel; l_1-l_6, first to sixth lemmas.

lower periphery. Occasionally a periclinal division has been observed in hypodermal cells towards the centre of the flower initial. A fourth sub-hypodermal cell situated immediately above the original three divides by walls at about 45°

to the vertical, and its derivatives also contribute to the formation of the primordium. The cells of the dermatogen invariably continue to divide only by the formation of anticlinal walls.

Under normal conditions, the spikelet differentiates 9 or 10 lemmas, each subtending a flower primordium, and an older spikelet thus shows 9 or 10 flower primordia in various stages of development. Rarely do more than five flowers develop to maturity on a spikelet; the more distal flower primordia fail to develop.

Plate 3, Figure 3, is a longitudinal section of a spikelet in which the seventh lemma is arising. This section is not quite median throughout its whole length, but it shows the relative development of the successive flower primordia. In Figure 5 a median longitudinal section of the same spikelet has been constructed by using different sections of the series through the spikelet for each flower primordium.

As the spikelet grows, the apex becomes less massive, mainly owing to a decrease in the number of cells in the meristem. This is seen in a comparison of the apices shown in Figures 3 and 4. The apex in Figure 3 is the youngest, whilst *B*, *D*, *C*, and *A* in Figure 4 are successively older. Details are given in the captions to the figures.

Cells of the apical meristem become vacuolated at an earlier age in older spikelets. The rate of cell division also decreases in the older meristems. Under normal conditions, further differentiation beyond the 10th lemma does not occur and possibly the withdrawal of materials from the apex may commence at this stage.

(*e*) *Differentiation of Flower Parts*

The young flower primordium in the rounded stage prior to differentiation of any floral parts has the same characteristic arrangement of cells as the apical meristems of the spike and spikelet. The dermatogen and hypodermis, as we noted previously and can now clearly observe, have been derived from the corresponding layers of the axis of the spikelet. The cells of the core have been derived from the sub-hypodermis, though occasionally some hypodermal cells have contributed. Development of the young flower primordium is illustrated in Figure 6 and Plate 4, Figure 2.

The palea arises by the periclinal division of several dermatogen and hypodermal cells (Figs. 6*D* and 7*A*, and Plate 4, Figs. 3-6), and is thus comparable in origin with the foliar-like organs described above. The area of initiation is a narrow band, about three dermatogen cells wide, extending around the adaxial or inner side of the flower primordium. The hypodermal cells usually undergo only one division and further development of the palea is by division of the derivatives of the dermatogen cells. Division is more rapid in the derivatives of the central one of the three original dermatogen cells, with the result that the young palea emerges as a ridge three cells thick. Development is most rapid in the two lateral areas and in its early stages the palea is a two-winged structure.

Very shortly after the initiation of the palea genesis of the lodicules and stamens occurs; lodicules originate in the manner of foliar structures, stamens as cauline structures.

When the palea is represented only by the first division of the initiating dermatogen and hypodermal cells periclinal division occurs in hypodermal cells very near the base of the opposite (abaxial) side of the primordium (Plate 4, Fig. 4). These periclinal divisions extend transversely along more or less the whole of the base of the abaxial surface, and constitute the first step in the formation of the lodicules. A little later or after the initiation of the stamens has commenced, periclinal divisions in the dermatogen occur in the areas between the anterior and lateral stamen initials. Further lodicule development is restricted to these two areas.

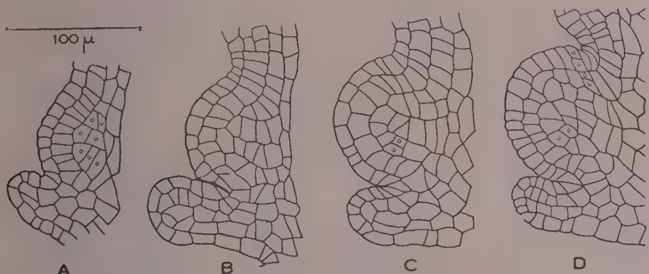

Fig. 6.—Radial longitudinal sections of developing flower primordia. *A*, periclinal divisions in cells of sub-hypodermis of spikelet axis; *B*, files of cells derived from division of sub-hypodermal cells; *C*, first division in sub-hypodermis of flower primordium which is probably origin of anterior stamen; *D*, origin of palea in periclinal divisions of dermatogen and hypodermal cells and division of sub-hypodermal cell initiating anterior stamen.

Almost immediately following the divisions in the hypodermis at the base of the primordium, periclinal divisions may be seen in the hypodermis nearer to the apex of the primordium. These are associated with the origin of the stamens. At the same time periclinal divisions also associated with origin of the stamens occur in cells of the sub-hypodermis. For the sake of clarity, the anterior stamen is taken to illustrate histogenesis; the origin of the lateral stamens is similar. Longitudinal sections which pass through the centre of the axis of the spikelet and the apex of the flower primordium, also pass through the centre of the anterior stamen. Such sections therefore show most clearly the origin of this structure.

In Figure 6*C*, a periclinal division of a sub-hypodermal cell probably represents the very first stage in stamen formation. In Figure 7*A*-*C* other sub-hypodermal cells have divided periclinally; in Figure 7*B* one hypodermal cell has also undergone periclinal division, whilst in 7*C* similar divisions have occurred in two hypodermal cells. In this figure and in Figure 5 and Plate 4, Figures 4 and 5, the files of cells derived from the sub-hypodermis clearly show that this layer is the centre of origin of the stamen.

The origin of the stamen is therefore comparable with that of the spikelet primordia and the flower primordia. It differs mainly in the more frequent periclinal divisions of the hypodermal cells. As far as could be ascertained, however, the hypodermal cells divided only once and the derivatives of the sub-hypodermal cells

contributed the main bulk of the stamen primordium. At no stage do the dermatogen cells divide by other than anticlinal walls. For a short period the stamen primordium is organized as a cauline meristem with reasonably well-defined dermatogen hypodermis and core. Differentiation of the sporogenous tissue and the anther sacs occurs early. These later developments have, however, been described by other workers.

After the stamens have developed as small papillae on the surface of the flower primordium the carpel has its beginning. Between the adaxial (upper) surface of the anterior stamen and the apex of the flower primordium a periclinal division takes place in one or two hypodermal and dermatogen cells (Figs. 7*C* and 8*A*).

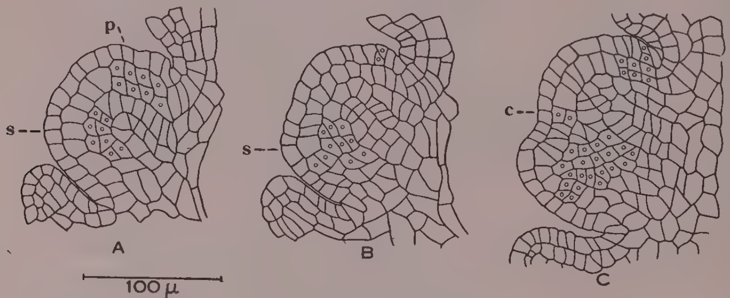

Fig. 7.—Radial longitudinal sections of flower primordia showing origin of palea and anterior stamen. *A*, periclinal divisions in four sub-hypodermal cells originating stamen (*s*) and in hypodermal cells initiating palea (*p*); *B*, periclinal division in hypodermal cell as well as in sub-hypodermal cells initiating stamen (*s*); *C*, files of cells derived from division of sub-hypodermal cells and the two hypodermal cells initiating the anterior stamen. A periclinal division in hypodermal cell initiating the carpel is shown at *c*.

Similar divisions occur in an arc extending about half-way around the apex. These divisions closely encircle the apex because the dividing cells are usually only three dermatogen cells removed from the apical dermatogen cell. From the palea to the tip of the apex there are also only about three dermatogen cells so that there are indeed very few cells left of the growing point of the flower primordium after the differentiation of the carpel (Fig. 8*B*). By repeated division of the dermatogen cells and their derivatives, the carpel emerges as a crescent-shaped collar (three cells thick) on the anterior side of the apex. The origin of the carpel is thus essentially the same as that of the leaf primordium, the lemma, and the palea. Derivatives of the hypodermal cells probably contribute less and the dermatogen cells more to the development of the palea and carpel than they do to the development of the foliar primordium and lemma.

As the carpel grows, periclinal divisions occur in the dermatogen at the edges of the crescent-shaped collar, extending it around to the posterior side of the apex and completely encircling it (Fig. 8*C*). Growth of the collar is more rapid on the anterior side so that the young carpel forms a cowl-shaped structure. Eventually development from the edges closes the base of the cowl and forms the loculus of

the ovary. Intermediate stages in the development of the carpel are illustrated in Figures 5 and 8, and Plate 4, Figures 5 and 6.

Following the differentiation of the carpel the apex of the flower primordium increases in size and its organization into dermatogen, hypodermis, and core may be again clearly seen (Fig. 8*C*; Plate 4, Fig. 6). Growth is more rapid on the posterior side so that it gradually becomes turned outwards. At the time of carpel formation the apex is inclined towards the axis of the spikelet. In older flower primordia it is directed vertically upwards and as growth continues more rapidly on the posterior (axis) side it gradually assumes a horizontal position, pointing outward from the spikelet axis, and finally points downwards. The apex forms the ovule. The archesporial cell is developed from the apical hypodermal cell and this occurs when the apex is pointing horizontally outwards from the spikelet axis.

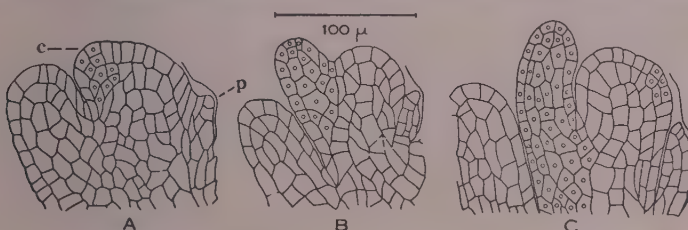

Fig. 8.—Radial longitudinal sections of flower primordia showing origin of carpel. *A*, division of dermatogen and hypodermal cells at (*c*) originating the carpel and at (*p*) the palea is developed; *B*, the young carpel developing; *C*, the carpel has encircled the growing point as shown by periclinal divisions in the dermatogen on the adaxial side of apex.

The outer and morphologically adaxial integument then arises by periclinal division of cells of the hypodermis followed by periclinal divisions in adjacent cells of the dermatogen. The outer abaxial integument and the two inner integuments arise similarly in the manner of foliar structures. Further development of the integuments is by division of the derivatives of the dermatogen cells. Periclinal divisions of hypodermal cells take place during the enlargement of the archesporial cell and form the nucellus. The archesporial cell becomes the megaspore mother cell.

V. Discussion

The similarity in the early histogenesis of the foliage leaf, glume, lemma, palea, lodicules, and carpel is striking. The difference between the mode of origin of these structures and the stamen is most marked. The origin of the stamen is similar to that of the lateral spikelet primordium and the flower primordium, and that of the vegetative bud as described by Rösler (1930) in *Triticum*, Kliem (1937) in *Avena*, and Sharman (1945) in *Agropyron*.

It is logical to conclude that the lateral spikelets are homologous with axillary vegetative shoots. They arise in the same way and are subtended by foliar primordia. The terminal spikelet develops directly from the apex of the vegetative

shoot and the organization of the apical meristem undergoes no fundamental change in this transition. The apical meristem of the lateral spikelets is constituted in the same manner as that of the vegetative meristem. The lowest glume of the apical spikelet is morphologically homologous with the foliar organs which subtend the lateral spikelets.

The differences in the histogenesis of the "foliar" structures in the floral region here described and the histogenesis of true foliage leaves as described by Rösler (1930), Kliem (1937), and Sharman (1945) are of a minor nature and possibly due for the most part to differences of interpretation. Rösler (1930) said, for instance, that the young leaf hump of *Triticum vulgare* is a purely dermatogen formation and that the first signs of its formation are periclinal divisions of a group of dermatogen cells. He then went on to say that, shortly afterwards or simultaneously, tangential walls appear in the cells of the layer beneath. Whilst the bulk of the leaf primordium tissue is derived from the dermatogen, he said that the cells of the layer beneath develop new cell walls at a slow rate. Sharman's description is very similar to that presented in this paper. The vertical depth of dividing dermatogen cells was given by Rösler as three in *Triticum* and by Sharman as two in *Agropyron*. The author found usually only one, sometimes two, and occasionally three, in the origin of the lemma.

The origin of the vegetative bud as described by Rösler, Kliem, and Sharman is also from the division of sub-hypodermal cells, as recorded here for the spikelets. Rösler found the organization of the apical meristem of the young plant a little different from that of the older plant in that in the young stages all the tissues internal to the dermatogen had a common origin. In the older apical meristem the layer within the dermatogen, i.e. the hypodermis, originated as a separate layer also. This was found when the vegetative axis was elongating to spike formation and in all subsequent developments. Rösler maintained that in *Triticum* the axillary primordia had at first an organization similar to that of the apical meristem of a young plant. Sharman also found periclinal divisions in the hypodermis at the centre of the primordium of developing axillary buds and said, "presumably these are destined to be the initials of the hypodermis of the future bud apex". In the origin of the spikelets and flower primordia, occasional periclinal divisions in the hypodermis were found and similar periclinal divisions occur a little more frequently in the formation of the stamen.

Rösler described and figured periclinal division in the apical cells of the hypodermis in the emerging axillary bud. Sharman found no such divisions in *Agropyron* nor did the author find any in the spikelet primordia. In the several minor differences of this nature which are found in the accounts of the histogenesis of the axillary bud of *Agropyron* by Sharman, of *Triticum* by Rösler, and of *Avena* by Kliem, the results of the present study of the floral region of *Triticum* agree most closely with Sharman's version.

The lemma is to be interpreted as a foliar appendage on the spikelet axis or rachilla. It arises in the same way as a foliage leaf and subtends a cauline structure. In both lemma and leaf, growth is at first mainly by apical merismatic activity and later by the division of cells in a zone near the base of the organ.

The flower primordium arises in essentially the same manner as that of the axillary vegetative bud and spikelet. It is also subtended by a foliar-like structure. The organization of its merismatic tissues is fundamentally the same as that of the vegetative axis. Laterally it produces members, some of which have a foliar-like and others a cauline-like origin. It must be regarded as the morphological equivalent of a leafy shoot, though its axis is very short.

The palea and lodicules are appendages with a foliar-like origin developed on the axis of the flower primordium.

The cauline mode of origin of the stamens is most interesting and supports the concept of the evolution of the stamen based on the telome theory advanced by Wilson (1937, 1942). Wilson concluded from studies of the vascularization of the stamen and palaeobotanical evidence that this organ has been derived by reduction from a branch system. Wilson (1937), however, argued: "If the leaf is the end result of the evolution of a major branch system, a logical conclusion from palaeobotanical studies, then the modern stamen is not homologous with the entire leaf as stated under the classical theory of the nature of the sporophylls of the flower; it is rather homologous with only part of a leaf and the term sporophyll may no longer be applied". It is not necessary to accept this argument to concede the relevance of his main conclusion. Sharman (1947, p. 33) noted that "the stamen primordia look like normal bud primordia and bear no resemblance at all to leaf primordia" in *Agropyron*.

The carpel, though similar in its early histogenesis to a foliage leaf and maybe the morphological equivalent of a leaf, is not comparable to a leaf folded along its midrib and bearing ovules along its margin as the classical theory postulates. The ovule terminates the branch system that constitutes the flower. The integuments are the last two structures which have a foliar-like origin formed on the main axis of this branch system; and the megaspore mother cell is derived from the apical cell of its hypodermis.

Histogenesis, therefore, strongly suggests that the flower in *Triticum* may be regarded as a reduced branch system subtended by the lemma. Foliar appendages, in the form of a palea, lodicules, and a carpel, are developed on the main axis of the system. The anthers are terminal microsporangia on lateral branches of the system, whilst the megasporangium is terminal on the main axis.

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Explanation of Plates 1-4

Plate 1

Morphology of the wheat spike

lp, leaf primordium; *sp*, spikelet primordium; *gl*, glume; *fp*, flower primordium; *s*, stamen; *c*, carpel; *p*, palea; *r*, lodicule ridge; *l*, lemma.

Fig. 1.—Apex of vegetative axis commencing to elongate prior to spike formation. Fourteenth leaf primordium at *lp*. × 35.

Fig. 2.—Apex further elongated with younger leaf primordia as crescentic ridges only. × 35.

Fig. 3.—Apex much elongated and leaf primordia showing as ridges. Spikelet primordia almost distinguishable. × 35.

Fig. 4.—Spikelet primordia in the axils of the leaf primordia give a "double ridge or ring" appearance. × 35.

Fig. 5.—Young spike showing double ridges of spikelet primordia and subtending leaf primordia at base. Towards apex spikelet primordia occur as rounded protuberances. × 24.

Fig. 6.—Young spike with spikelet primordia developing in acropetal succession. The leaf primordia subtending basal spikelets are still discernible. × 24.

Fig. 7.—Spikelet primordia with two empty glumes and first lemma developed as ridges; note apical spikelet. × 24.

Fig. 8.—Spikelet primordia showing two empty glumes and first and second lemmas. × 24.

Fig. 9.—Spikelet primordia about same stage as in Plate 1, Figure 7, viewed directly. × 26.

Fig. 10.—Direct view onto spike with spikelets in which first flower primordium is developed. In the most advanced spikelet the flower primordium in the axil of the first lemma is a well-developed rounded structure and is just appearing in the axil of the second lemma. × 26.

Fig. 11.—Portion of a spike 3.5 mm long showing spikelets in which fifth lemma is just arising; flower primordia in axils of first and second lemma have differentiated a palea, three stamens, and carpel, whilst those in axil of third lemma have not yet differentiated any parts. × 30.

Fig. 12.—Anterior view of young flower primordium showing three young stamens and carpel. Lodicules represented by ridge along anterior surface of primordium. × 65.

Fig. 13.—Posterior view of young flower primordium showing palea, two lateral stamens, and carpel in centre. View of anterior stamen is obscured. × 32.

Fig. 14.—Anterior view of older flower primordium in which palea extends above stamens and lodicules are well developed. × 32.

Plate 2

Photomicrographs of longitudinal sections of spike in plane of leaf insertion

d, dermatogen; *h*, hypodermis; *lp*, leaf primordium; *sp*, spikelet primordium.

Fig. 1.—Vegetative apex as it commences to elongate prior to spike formation, showing dermatogen, hypodermis, and central core. Compare with Plate 1, Figure 1. × 262.

Fig. 2. Vegetative apex further elongated showing origin of leaf rudiments. Compare with Plate 1, Figure 2. × 173.

Fig. 3.—Apex much elongated, showing some 12 leaf rudiments prior to formation of spikelet initials. Compare with Plate 1, Figure 3. × 107.

Fig. 4.—Portion of young spike showing two leaf initials and origin of spikelet primordium in periclinal divisions of cells of the sub-hypodermis. × 378.

Plate 3

Photomicrographs of sections of spike and spikelets

lp, leaf primordium; fp_1-fp_6, first to sixth flower primordia; gl_1, first glume; gl_2, second glume; l_1, l_2, etc., first and subsequent lemmas.

Fig. 1.—Longitudinal section of portion of spike with spikelet primordia as rounded structures and showing subtending leaf initials. × 93.

Fig. 2.—Longitudinal section of young apical spikelet showing third lemma arising, a large flower primordium in axil of first lemma, and one originating in the axil of the second lemma. Compare with Plate 1, Figure 10. × 177.

Fig. 3.—Longitudinal section of spikelet in which the seventh lemma is arising. Not quite median throughout whole length but showing relative development of successive flower primordia. × 88.

Fig. 4.—Transverse section of apex of spikelet in which dermatogen, hypodermis, and central core are defined. The several periclinal divisions in the hypodermal cells are associated with the edge of a lemma primordium. × 292.

Fig. 5.—Transverse section of apex of spikelet showing origin of lemma in periclinal divisions of hypodermis and dermatogen. × 292.

Plate 4

Photomicrographs of median longitudinal section of apex of spikelet and flower primordia

l, lemma; *fp*, flower primordium; *s*, anterior stamen; *c*, carpel; *gl*, glume; *p*, palea.

Fig. 1.—Apex of spikelet in which dermatogen, hypodermis, and core are shown. The origin of the ninth lemma is seen in the periclinal division of a cell of the dermatogen. A periclinal division in three cells of the sub-hypodermis just above the eighth lemma is the initiation of a flower primordium. × 295.

Fig. 2.—Young flower primordium showing continuity of dermatogen and hypodermis with these layers of the axis of the spikelet and the central core consisting of files of cells derived from the sub-hypodermis. × 295.

Fig. 3.—Flower primordium showing origin of the palea and the anterior stamen. × 295.

Fig. 4.—Flower primordium showing origin of palea in periclinal divisions of hypodermal cells; anterior stamen as papilla with files of cells derived from sub-hypodermis; and on abaxial side near lemma periclinal division of hypodermal cell associated with origin of lodicules. × 295.

Fig. 5.—Flower primordium comparable with that shown in Figure 4, but further developed. × 295.

Fig. 6.—Flower primordium in which carpel has arisen; palea, apex, carpel, anterior stamen, and lemma shown. × 193.

HISTOGENESIS IN TRITICUM AESTIVUM

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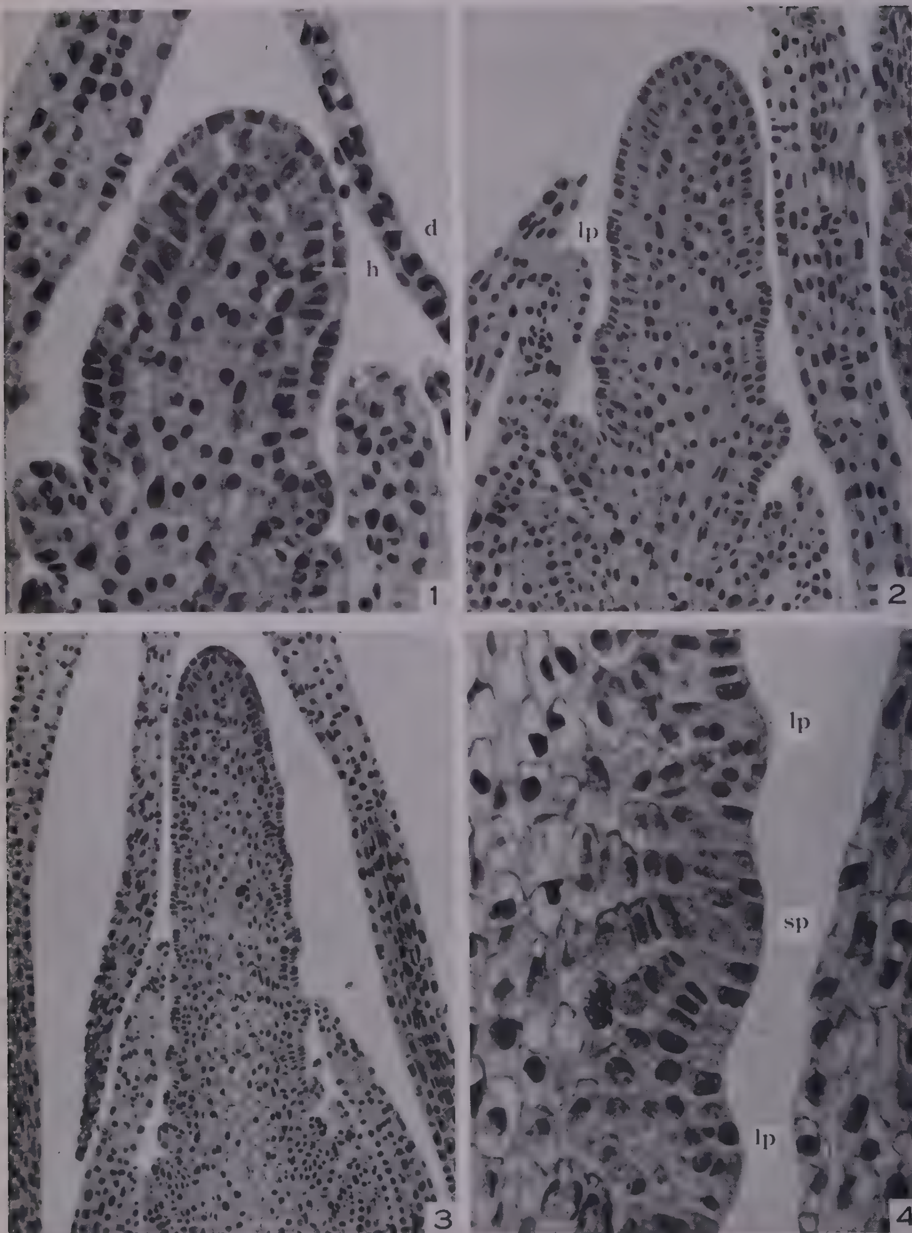

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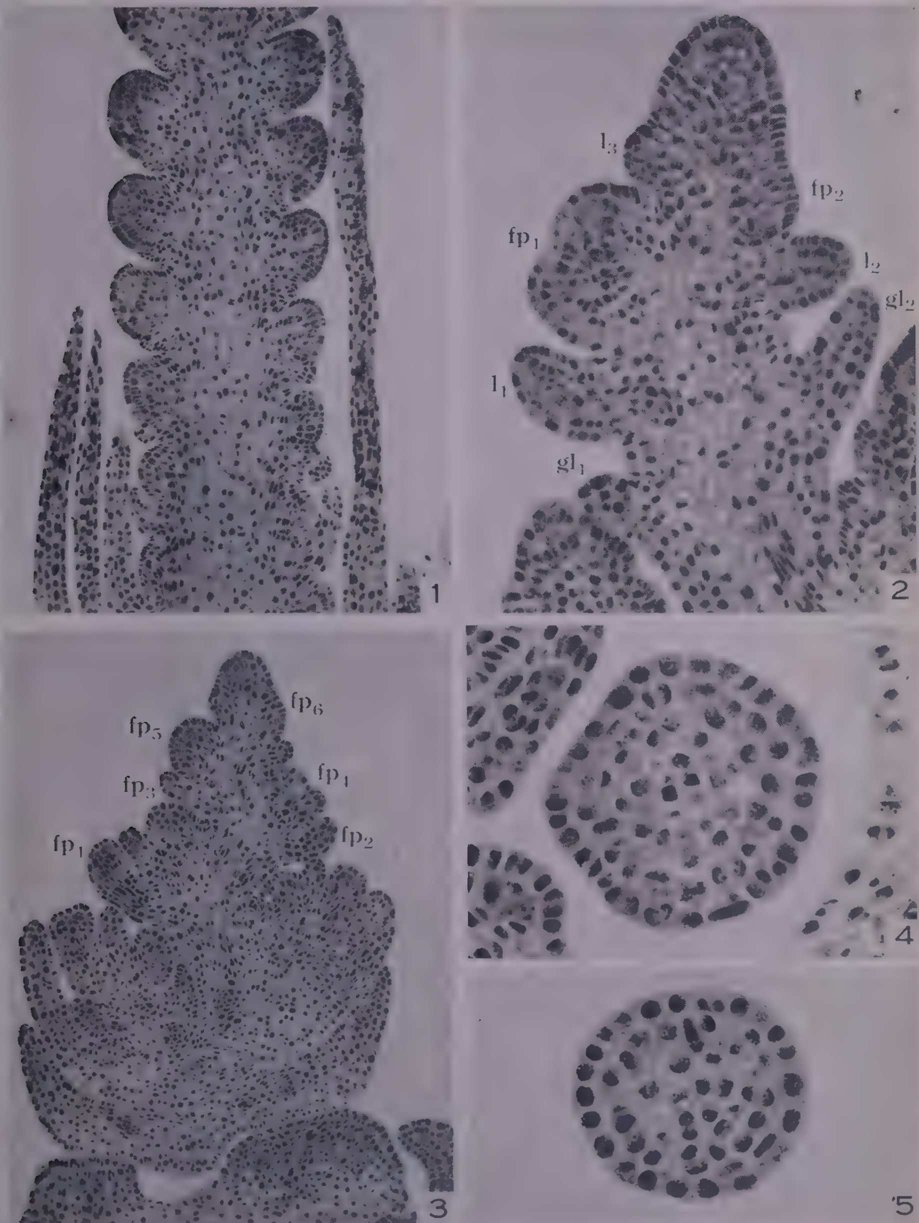

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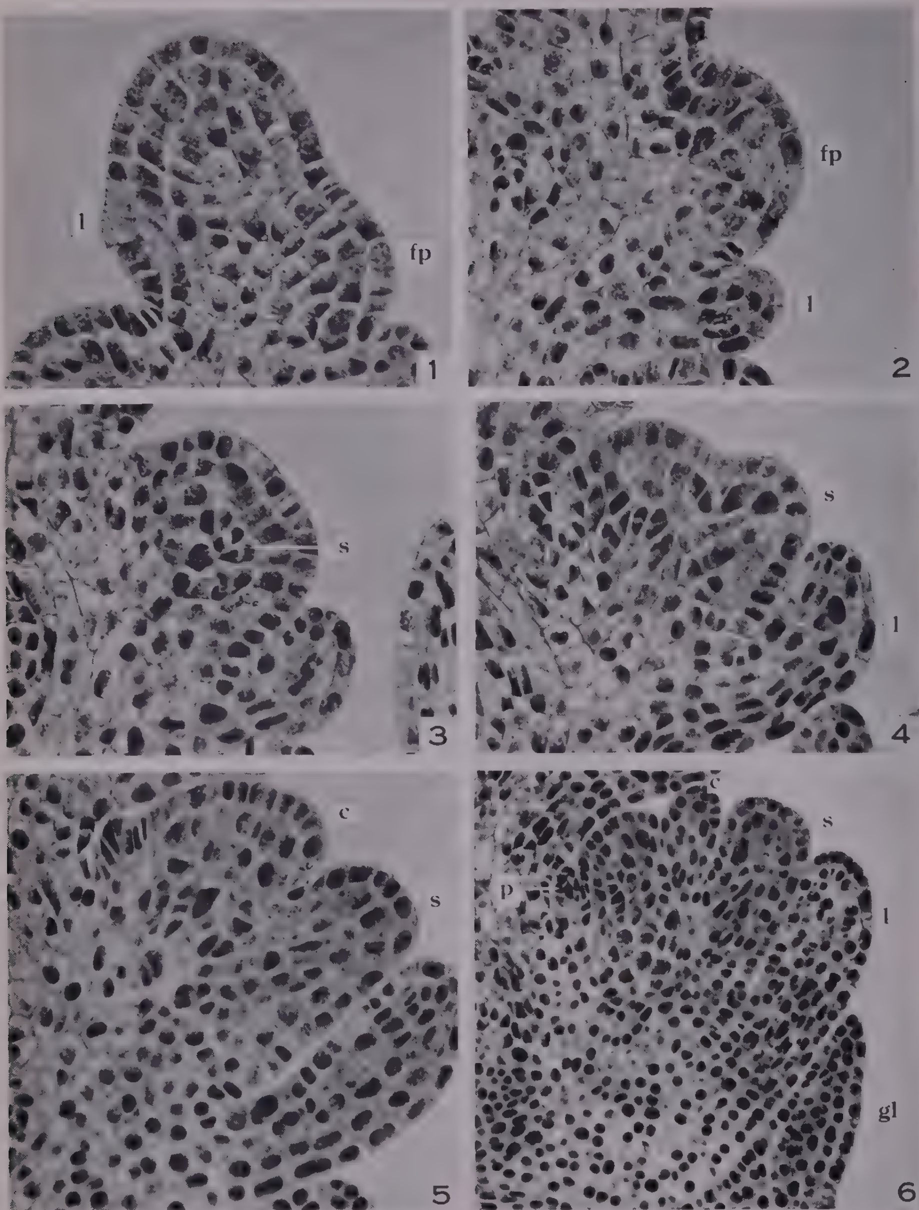

THE ANATOMY OF BARK

II. OIL GLANDS IN EUCALYPTUS SPECIES

By M. Margaret Chattaway*

[*Manuscript received September* 10, 1954]

Summary

Spherical oil glands of lysigenous origin have been observed as a conspicuous feature of the phloem of 41 species of *Eucalyptus*. They occur in seven series of species, six of which are very closely related.

Details of their development from rays of phloem parenchyma are described and their contents and functions discussed.

I. Introduction

In 1922, Welch gave an account of the occurrence of oil glands in certain species of *Eucalyptus*. At that date little work had been done on the anatomy of eucalypt bark; his list is by no means complete, and he did not grasp the significance of their distribution.

More recently, these oil glands were mentioned by Chattaway (1953), who showed that they were present only in certain closely related species. This investigation has been continued, and it is now possible to give a much fuller list of species than that given by Welch, and to elucidate some points in their development that he did not make clear.

The oil glands are spherical bodies of variable size; they may be scattered through the outer phloem or aggregated into the wedges of parenchyma which accommodate the outer phloem to the increasing diameter of the stem. They are not lined with an epithelium, but often contain the remains of tissues which have disintegrated during their growth and development. Their presence gives great pungency to the bark of certain species. Oil from the bark of *E. macarthuri* was examined by Smith (1916) and was found to contain 0·12 per cent. of oil, mainly geranyl acetate, and to be similar to that found in the leaves. Little work has, however, been done on the bark oils and the literature is singularly bare of reference to them. Welch (1922) gives the solubility of the oils in the species he investigated, but does not deal with their chemical nature. It would appear that some of the species (e.g. *E. cinerea*, *E. cephalocarpa*) which have very abundant oil glands in the bark might prove of commercial value.

Welch suggests that the oil glands in the genus *Eucalyptus* are for protection against insect or fungus attacks, but this does not seem to be a satisfactory explanation, and he advances no data to show that these species are less susceptible to insect or fungal attack than those without oil glands in the bark. The oil glands have a certain diagnostic value in that they occur within a few groups of species, but these groups can be equally well defined on other features, and the oil glands are not sufficiently different in number or distribution to enable any distinction between species to be made.

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II. Distribution

Oil glands have been observed in only 43 out of 270 species of *Eucalyptus*; they are restricted to the groups indicated in Table 1.

Several of the species in which oil glands have not been observed have been available only in small quantities, and it is possible that oil glands might be found if older material, or bark from a greater number of trees, could be examined.

The list of species with oil glands includes 13 out of the 15 species mentioned by Welch (1922). The remaining two, *E. nova-anglica* Deane & Maiden* and *E. pulverulenta* Sims, have not been available for examination in this investigation, but both are in groups in which oil glands are common.

Welch gives a list of species in which oil glands were not observed, but only three of these, *E. camphora*, *E. globulus*, and *E. maideni*, are from the groups in which they might be expected. Oil glands have now been observed in these three species, but they are sporadic in occurrence and could easily be missed unless material from a number of different trees was examined. Welch's list of species without oil glands is very incomplete, for the most striking feature of the distribution is their restriction to seven out of the 47 recognized series of eucalypt species. The significance of this close relationship of the majority of species with oil glands to one another was entirely missed by Welch.

The most unexpected occurrence of oil glands is in the bark of three species of the Eudesmieae, *E. eudesmioides*, *E. similis*, and *E. tetrodonta*. The Eudesmieae is far removed in most classifications from the other series in the list. It is considered to be one of the links between the more primitive eucalypts and the genus *Angophora*. The bark structure appears to be similar to that of *E. cinerea*, the rhytidome showing marked expansion of the parenchyma, and the oil glands developing in considerable numbers scattered through the phloem, and not being confined to the parenchyma wedges, which are small and inconspicuous. The other members of this group which were available for examination were, except for *E. baileyana*, only from single specimens of very young trees, and the absence of oil glands from their bark would need to be confirmed from more numerous and older specimens.

The Subexsertae has two subgroups, the Argophloiae, which resembles the series Exsertae, and the Semidecorticatae, which resembles more closely the series Microcarpae. The former contains *E. alba* (now including *E. platyphylla*) and *E. pallidifolia* F. Muell. and *E. pastoralis* S. le M. Moore; no material of the last two was available for examination. Of the four species in the Semidecorticatae, *E. studleyensis* is reputed to be a hybrid of *E. camaldulensis* Dehn. and *E. ovata*. The bark of the only four trees known (from Studley Park, Kew, Vic.) was examined, and was found to be closer to *E. camaldulensis* in bark structure than to *E. ovata*. The other three species in the Semidecorticatae have a bark structure which is similar to that of the other groups with oil glands. The Subexsertae thus appears to be an unnatural grouping, and might well be subdivided.

* Since this paper was submitted for publication material of this species has been examined. Oil glands are numerous.

TABLE 1

DISTRIBUTION OF OIL GLANDS IN EUCALYPTUS SPP.

	With Oil Glands	Oil Glands Not Observed
I. EUDESMIEAE 5 Species not available for examination	*eudesmioides* F. Muell. (1)* *similis* F. Muell. (2) *tetrodonta* F. Muell. (3)	*baileyana* F. Muell. (1) *erythrocorys* F. Muell. (1) *tetragona* F. Muell. (1)
XVI. SUBEXSERTAE 1 Species not available for examination	*aggregata* Deane & Maiden (7) *camphora* R. T. Baker (2) *ovata* Labill. (22)	*alba* Reinw. (including *platyphylla* F. Muell.) (7) *studleyensis* Maiden (a hybrid with a very limited distribution) (4)
XVII. MICROCARPAE 2 Species not available for examination	*acaciaeformis* Deane & Maiden (11) *maculosa* R. T. Baker (19) *nicholi* Maiden & Blakely (2)	Nil
XVIII. GLOBULARES 15 Species, including four reputed hybrids, not available for examination	*angophoroides* R. T. Baker (4) *antipolitensis* Trabut (1) *banksii* Maiden (2) *bicostata* Maiden, Blakely & Simmonds (7) *cordata* Labill. (2) *cordieri* Trabut (2) *dalrympleana* Maiden (5) *dunni* Maiden (1) *elaeophora* F. Muell. (31) *globulus* Labill. (15) *goniocalyx* F. Muell. (40)	*megacarpa* F. Muell. (3) *preissiana* Schauer (1)
XVIII. GLOBULARES (*Continued*)	*gunnii* Hook. f. (4) *maideni* F. Muell. (3) *mannifera* (A. Cunn. Herb.) Mudie (4) *morrisbyi* Brett (1) *nitens* Maiden (2) *perriniana* (F. Muell.) Rodway (4) *rubida* Deane & Maiden (19) *st johnii* R. T. Baker (1) *stuartiana* F. Muell. (including *bridgesiana* R. T. Baker (15) *unialata* Baker & Smith (2) *urnigera* Hook. f. (2)	
XIX. SEMIUNICOLORES 3 Species not available for examination	*subcrenulata* Maiden & Blakely† (4) *johnstoni* Maiden (7)	*kitsoniana* (Luehmann) Maiden (2) *neglecta* Maiden (1)
XX. VIMINALES 2 Species not available for examination	*badjensis* de Beuzeville & Welch (1) *benthami* Maiden & Cambage (1) *huberiana* Naudin (6) *macarthuri* Deane & Maiden (3) *smithii* R. T. Baker (8) *viminalis* Labill. (69)	*quadrangulata* Deane & Maiden (5)
XXI. ARGYROPHYLLAE 5 Species not available for examination	*cephalocarpa* Blakely (3) *cinerea* F. Muell. (4) *nova-anglica* Deane & Maiden (3)	Nil

* Numbers in brackets are the numbers of specimens examined. † Early developmental stages only.

Oil glands have not been observed in *E. preissiana* or *E. megacarpa* although they are present in the other 21 species of the Globulares which were examined. Blakely (1934), however, refers to these two species as occupying an anomalous position in the Globulares.

Of the six species included by Blakely in the Semiunicolores only four were available for study. Only one of these is at all common, and this one, *E. johnstoni*, contains oil glands; they have also been observed, though sparsely, in *E. subcrenulata*. *E. kitsoniana* and *E. neglecta* have only been available as small samples in which no oil glands have been observed. It is possible that investigation of further material might show them to conform to the general structure of the group.

III. Occurrence in the Bark

Oil glands occur as a tertiary development in the secondary phloem of some species of *Eucalyptus*; that is, though they occur in the secondary phloem they are not formed by the cambium, nor do they arise at the time the fibres and sieve tubes of the secondary phloem are differentiated. It has already been shown (Chattaway 1953) that the phloem parenchyma and rays remain potentially meristematic until they are cut off by periderm formation. It is in this tissue that the oil glands develop, usually in the parenchyma but sometimes in the rays.

Welch (1922) describes the oil glands in *E. macarthuri*, on which he conducted his developmental studies, as arising "in the broader medullary rays", and in a later paragraph he described the rays as consisting of a single layer of cells which broaden out about half-way to the cortex. In very young stems this is the case, and the ray tissue merges into the cortical in a broad wedge, in which it is very difficult to say where the ray ends and the cortex begins. But this is not the case in older stems, where successive periderms have cut away all the cortical tissue. At this stage the increasing girth of the tree has caused stresses in the outer phloem, under the stimulus of which the parenchyma cells enlarge and divide by radial walls to form large wedges of tissue in which the origin of the tangential files of cells can easily be traced (Plate 1, Figs. 1-3). On cross sections they might be confused with the wedges formed by the primary medullary rays, but are quite distinct from them in origin, and are always bounded on the outer side by a layer of phellem and not by an epidermis. They very seldom arise wholly from ray tissue, though occasionally a few enlarged ray cells may become incorporated in them. Usually the rays border or traverse them, often taking a sinuous course (Plate 1, Figs. 1-3). This structure is less evident when the phloem is examined in tangential longitudinal sections, as the parenchyma wedges then appear as spindle-shaped masses and are very similar in size and shape to the rays of certain large rayed woods. The tangential arrangement of their cells can still be seen in tangential longitudinal sections (Plate 1, Figs. 4 and 5; Plate 2, Fig. 1) and their true nature can be easily observed by comparison with cross sections. The rays of eucalypts are always small; in the species illustrated they can be seen bordering the parenchyma wedges and occasionally traversing them (arrows in Plate 1, Figs. 1, 2, and 4). It is in this parenchymatous tissue that the oil glands are most commonly formed.

In some species they appear to be confined to it and are seldom found elsewhere in the phloem; in others they occur scattered through the phloem (Plate 2, Fig. 2), commonly developing from the parenchyma but sometimes from the ray cells (Plate 2, Figs. 3 and 4). The scattered arrangement is characteristic of only a few species, *E. eudesmioides*, *tetrodonta*, *similis*, *nicholi*, *maculosa*, *rubida*, *mannifera*, *dalrympleana*, *cinerea*, and *cephalocarpa*. Four of these, *E. maculosa*, *dalrympleana*, *rubida*, and *mannifera*, have well-developed radially elongated phelloderm. This feature is absent from all the other species except *E. viminalis* and *E. unialata* in both of which it is sporadic, being well developed in some samples and absent from others. *E. viminalis* is one of the more variable eucalypt species in both its

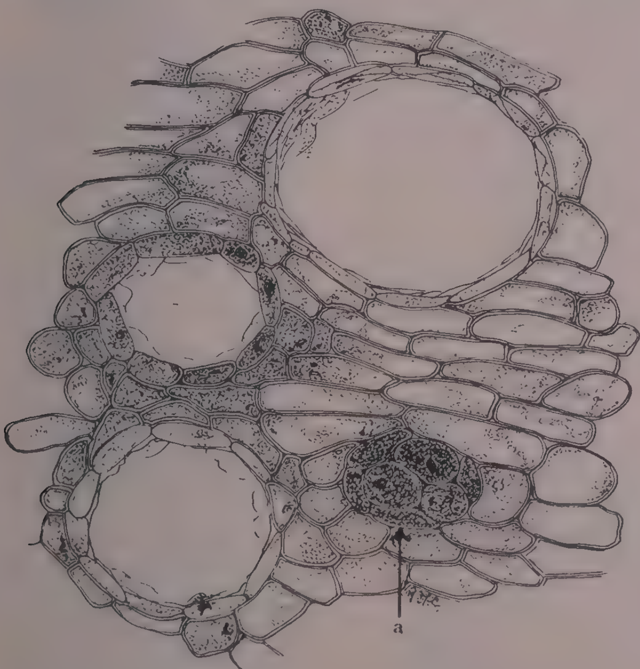


Fig. 1.—*E. cinerea* F. Muell. Development of oil glands in parenchyma. Tannin content of cells increases in initial stages. *a*, earliest stage. × 370 approx.

morphology and its wood and bark anatomy. There appears to be no close correlation between radially elongated phelloderm and scattered oil glands, for the remaining four species are without the radially elongated cells and yet have very numerous scattered oil glands. In the species with wide parenchyma wedges, however, there does seem to be some slight correlation between the wedges and oil glands, for these do not develop in any great number in samples with small wedges and are absent from areas in which the wedges do not develop.

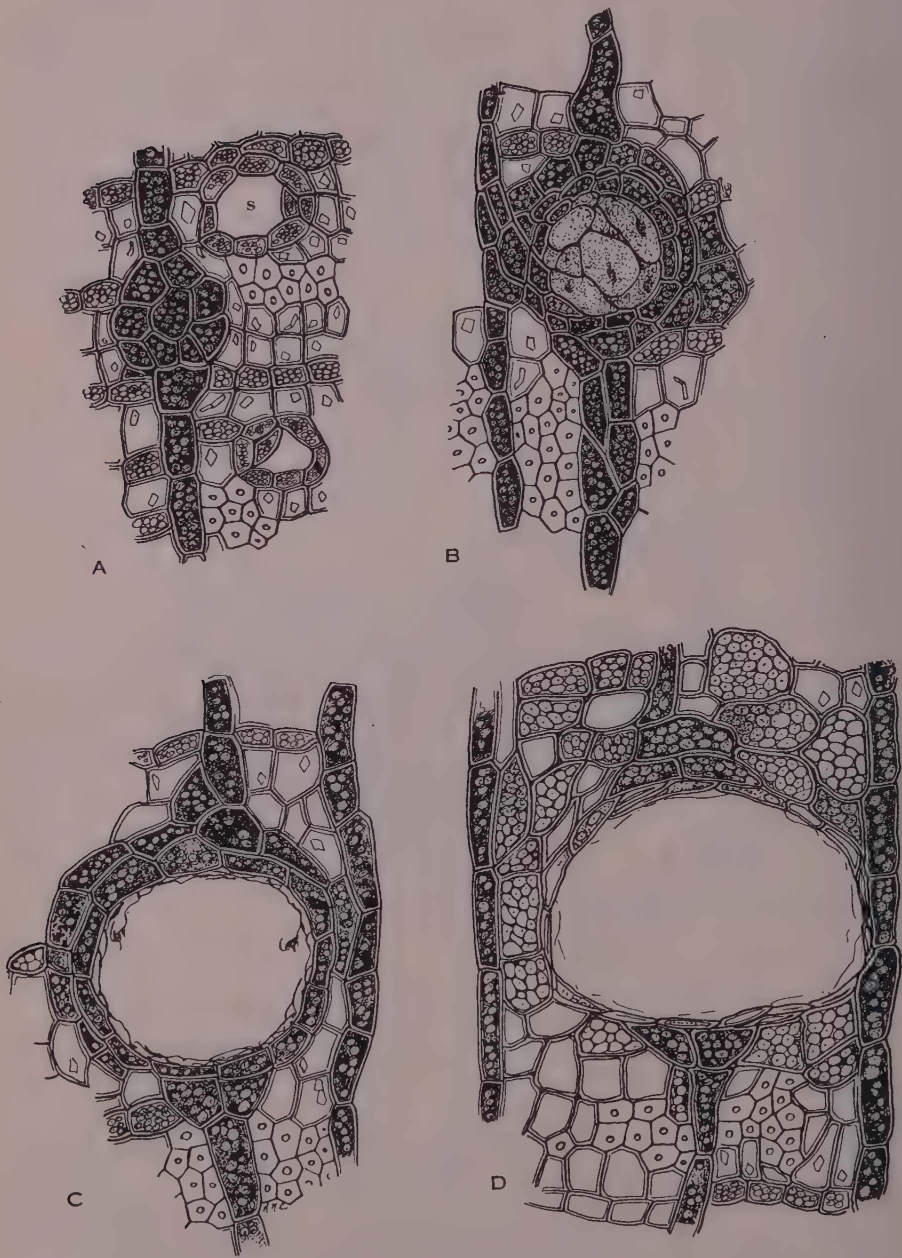
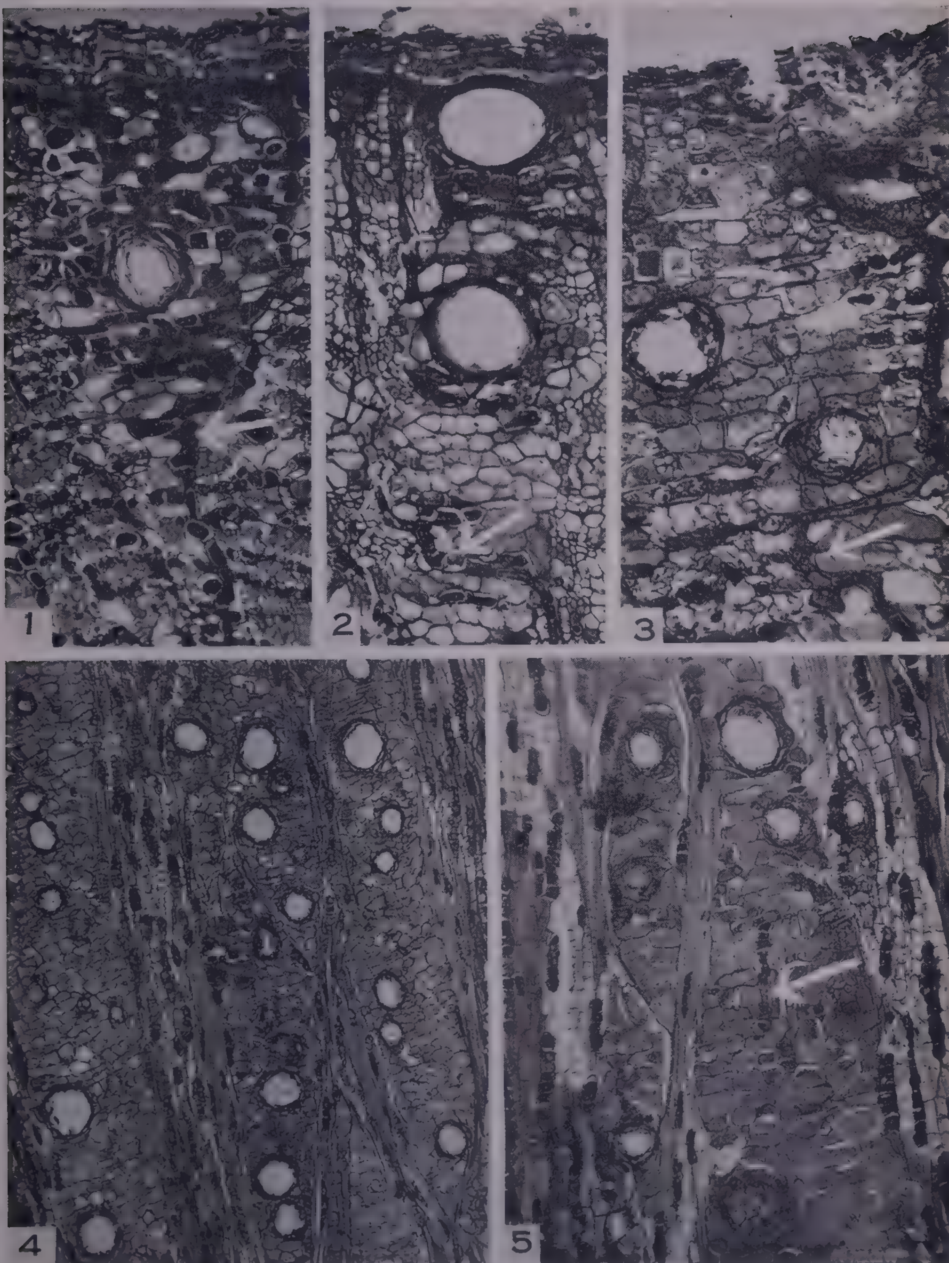
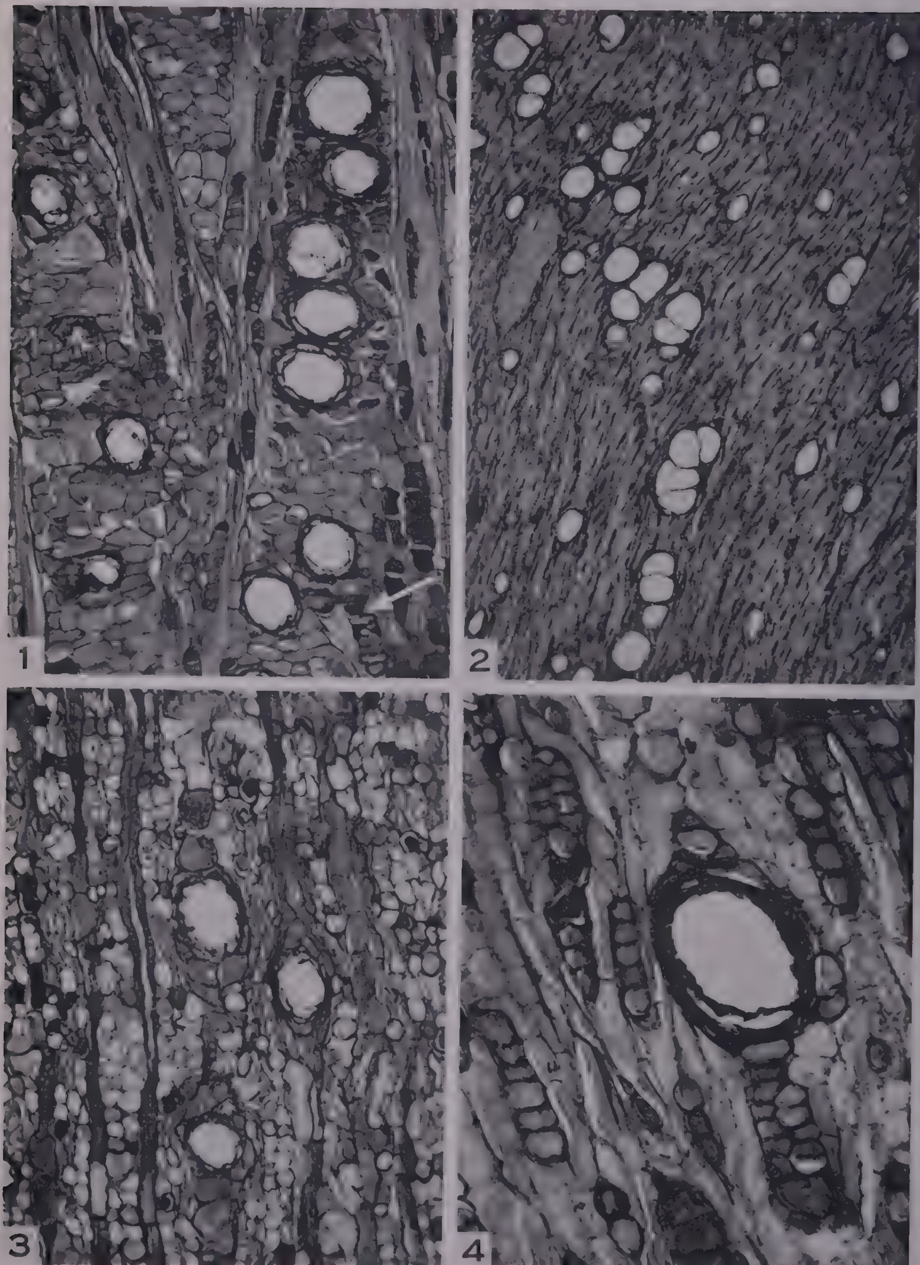


Fig. 2.—*E. cinerea* F. Muell. Development of oil glands in rays. Parenchyma and rays are packed with starch; ray cells contain tannin. *s*, sieve tube. × 370 approx.

THE ANATOMY OF BARK. II



THE ANATOMY OF BARK. II



IV. Development

Oil glands develop by subdivision of highly tanniniferous ray or parenchyma cells, which may also contain starch when they are situated in the outer phloem (Figs. 1 and 2). Certain cells of the rays, or more usually of the parenchyma, subdivide to form a group of cells; these subsequently enlarge and then disintegrate. Welch (1922) suggests that the development is "probably the same as in leaf oil ducts, where the early stages are schizogenous, subsequently become lysigenous, the mature cavity being therefore schizo-lysigenous". In *E. cinerea*, in which the development was most closely studied, no schizogenous stage could be observed, disintegration following quickly on the stage shown in Figure 2*B*, to give that shown in Figures 2*C* and 2*D*. The layer of cells which surrounds the cavity serves merely to differentiate it sharply from the surrounding tissue. There is no epithelium, but the glands are often lined with shreds of wall from the disintegrating cells. The absence of intercellular spaces, which is one of the characteristics of phloem tissue, may account for the omission of the schizogenous stage from the glands of the bark, even in species in which it is present in those of the leaves.

V. Acknowledgments

The author would like to acknowledge her debt to all who have assisted in this work by sending bark samples and by criticism and advice.

VI. References

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Explanation of Plates 1 and 2

Plate 1

Fig. 1.—*E. cordata*. Cross section of outer phloem, showing parenchyma wedge containing oil gland and (marked by arrow) ray taking sinuous course alongside. × 90.

Fig. 2.—*E. ovata*. Cross section of outer phloem, showing tangential alignment of cells in parenchyma wedge and ray (at arrow) crossing it. × 76.

Fig. 3.—*E. macarthuri*. Similar to the preceding. The origin of the wedge from tanniniferous parenchyma is clearly shown. × 138.

Fig. 4.—*E. macarthuri*. Tangential longitudinal section of outer phloem showing spindle shape of parenchyma wedges and the restriction of oil glands to them. × 51.

Fig. 5.—*E. macarthuri*. Tangential longitudinal section showing rays bordering wedge, and (at arrow) traversing it. × 87.

Plate 2

Fig. 1. *E. macarthuri*. Tangential longitudinal section of outer phloem showing oil glands in parenchyma wedges, small rays bordering the wedges and (at arrow) traversing one. × 83.

Fig. 2.—*E. maculosa*. Tangential longitudinal section of outer phloem showing scattered oil glands developing independently of parenchyma wedges. × 26.

Fig. 3.—*E. dalrympleana*. Cross section showing three oil glands, two developing from ray tissue and one from parenchyma. × 98.

Fig. 4.—*E. maculosa*. Tangential longitudinal section of outer phloem, showing oil gland developing in ray tissue. × 185.

THE ANATOMY OF BARK

III. ENLARGED FIBRES IN THE BLOODWOODS (EUCALYPTUS SPP.)

By M. MARGARET CHATTAWAY*

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Summary

Immensely enlarged fibres which are characteristic of certain bloodwoods separate them clearly from other species with which they are usually associated in the systematic classification of the genus *Eucalyptus*. Separation of the two types of bloodwood herein described agrees closely with a regrouping recently suggested on morphological characteristics.

Other eucalypts with large bark fibres are described briefly and their relationships considered.

I. INTRODUCTION

The two series into which the bloodwoods are divided by Blakely (1934)—the Corymbosae and Corymbosae-peltatae—are unnatural ones, whether the species they contain are considered from a morphological or an anatomical point of view. Within each there are two groups of species that are distinctive in appearance both in the field and in the colour of their woods.

In a recent investigation of the bark anatomy of this genus (Chattaway 1953) the peculiarities of the bloodwoods were briefly discussed and the development of the immense fibres of some species described. Since that time more species have been available for study and for comparison with material from other groups of *Eucalyptus* species. The present work is an attempt to assess the bark anatomy of the bloodwoods and to relate it to other *Eucalyptus* species which have somewhat similar peculiarities.

II. MATERIAL

The following material has been examined, the numbers in brackets referring to the numbers of specimens available for examination.

Smooth-barked Species

CORYMBOSAE: *E. aspera* F. Muell. (1); *E. clavigera* A. Cunn. (1); *E. confertiflora* F. Muell. (5); *E. gilbertensis* (Maiden & Blakely) S. T. Blake (1); *E. grandifolia* R. Br. (2); *E. papuana* F. Muell. (9); *E. tessellaris* F. Muell. (6).

CORYMBOSAE-PELTATAE: *E. citriodora* Hook. (4); *E. maculata* Hook. (11); *E. nowraensis* Maiden (2); *E. torrelliana* F. Muell. (4).

Rough-barked Species

CORYMBOSAE: *E. abbreviata* Blakely & Jacobs (1); *E. abergiana* F. Muell. (5); *E. dichromophloia* F. Muell. (now containing *E. erythrophloia* Blakely (Blake 1953)) (8); *E. ferruginea* Schauer (2); *E. ptychocarpa* F. Muell. (1); *E. setosa* Schauer (2); *E. terminalis* F. Muell. (1).

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CORYMBOSAE-PELTATAE: *E. bloxomei* Maiden (2); *E. calophylla* R. Br. (15); *E. eximia* Schauer (2); *E. ficifolia* F. Muell. (6); *E. gummifera* (Gaertn.) Hochr. (6); *E. haematoxylon* Maiden (3); *E. intermedia* R. T. Bak. (3); *E. jacobsiana* Blakely (1); *E. peltata* Benth. (10); *E. polycarpa* F. Muell. (8); *E. trachyphloia* F. Muell. (2); *E. watsoniana* F. Muell. (1).

Three species of the Corymbosae and five of the Corymbosae-peltatae were not available for examination.

The following large-fibred species will also be discussed:

MINIATAE: *E. miniata* A. Cunn. (2); *E. phoenicea* F. Muell. (1).

SUB-CORNUTAE: *E. redunca* Schauer (3); *E. wandoo* Blakely (2).

DUMOSAE: *E. accedens* W. V. Fitzgerald (4).

EXSERTAE: *E. parramattensis* Hall (1).

PANICULATAE: *E. cloeziana* F. Muell. (11).

FRAXINALES: *E. planchoniana* F. Muell. (11).

PIPERITALES: *E. congener* Maiden & Blakely (1); *E. linearis* Dehn. (2); *E. risdoni* Hook. f. (2); *E. tasmanica* Blakely (2).

PSATHYROXYLA: *E. haemastoma* Smith (3); *E. micrantha* DC. (9); *E. rossii* Baker & Smith (9).

III. Smooth-barked Bloodwoods

The details of the two series, Corymbosae and Corymbosae-peltatae, have already been described in general terms (Chattaway 1953). The deciduous and semi-deciduous species, from whichever series they come, have a very uniform type of structure. Their phloem consists of tangentially extended fibre bundles of varying width, often extending across several rays (Plate 1, Fig. 1). Each is ensheathed by a conspicuous layer of crystalliferous parenchyma which is thickened on the walls contiguous to fibres and other crystalliferous cells, and thin-walled only where it touches other parenchyma cells (Plate 1, Fig. 2). Each bundle is separated from adjacent fibre bundles by phloem parenchyma in which the sieve tubes usually occur. During the growth of the stem this parenchyma expands considerably in the outer phloem, separating the bundles. In most of the species examined this expansion takes the form of tangentially stretched cells which take a tangential or obliquely radial course through the outer phloem (Plate 1, Figs. 1, 3, 4, and 5), disturbing the course of the rays but only occasionally involving individual ray cells in their enlargement (Plate 1, Fig. 5). An interesting feature of these expanded parenchyma cells is that their walls contain conspicuously bordered pits. The walls are often very much thickened, and it is in such thick-walled cells that the bordered pits are most easily seen (Plate 1, Fig. 3; Plate 2, Figs. 1 and 2). This loosely constructed tissue is shed in thin strips, or flakes away as new periderms are formed throughout the trunk in the totally smooth species, or is retained as a "stocking" on the basal parts of the semi-deciduous species.

This structure is found in most of the species mentioned above, with slight variation from sample to sample in the amount of parenchyma expansion and the tangential extent of the fibre bundles. These variations are individual rather than specific and the species would be very difficult to separate on bark structure.

E. maculata usually has greater and more widespread parenchyma expansion and less sclerosis than the other species (Plate 2, Fig. 3). The rough basal bark of some

TABLE 1

DIAMETERS OF BLOODWOOD FIBRES (EUCALYPTUS SPP.)

Species	No. of Samples	Average Diameter (μ) of			
		Enlarged Fibres		Normal Fibres	
		Radial	Tangential	Radial	Tangential
SMOOTH-BARKED SPECIES					
aspera	1			25	25
clavigera	1			25	25
confertiflora	5			27	23
gilbertensis	1			42	34
grandifolia	2			38	30
papuana	9			42	38
tessellaris	6			57	40
citriodora	4			30	25
maculata	11			45	40
nowraensis	2	210	152		
torrelliana	4			27	27
ROUGH-BARKED SPECIES					
abbreviata	1	171	210		
abergiana	5	290	250		
dichromophloia	8	300	200		
ferruginea	2	175	125		
ptychocarpa	1	230	170		
setosa	2	300	170		
terminalis	1	300	190		
bloxomei	2	152	95		
calophylla	15	250	170	40	30
eximia	2	152	95		
ficifolia	6			46	40
gummifera	6	300	200		
haematoxylon	3	114	114		
intermedia	3	280	250		
jacobsiana	1			20	20
peltata	10	245	190		
polycarpa	8	290	170		
trachyphloia	1	210	155		
watsoniana	1	210	123		

species is of a close texture, the rhytidome layers being cut off by closely spaced periderms, with little subsequent parenchyma expansion. The retained rhytidome

cracks under the stress of the expanding stem diameter, and may produce a very characteristic bark pattern, as in *E. tessellaris*.

The fibres of all the species mentioned above, except *E. nowraensis*, are small in cross-sectional diameter, the largest observed being up to 40 μ in tangential diameter. Table 1 gives the approximate diameters of the largest fibres observed; the measurements are an average of six of the largest fibres to be found in a cross section; they give a good picture of the maximum fibre size attained in this group and show the great contrast between the smooth-barked and rough-barked species.

E. nowraensis is a semi-deciduous species which has the external form of *E. maculata* but the phloem pattern of the rough-barked species. It is, however, now assumed to be a hybrid between *E. maculata* and *E. gummifera*, the phloem features of both parents appearing in the bark, the large fibres of *gummifera* being combined with the expanded phloem parenchyma which is such a distinctive feature of *maculata*. This is shown in Figure 1.

A palisade of radially elongated cells occurs locally in some specimens of the species *E. aspera*, *E. confertiflora* (Plate 2, Fig. 4), and *E. papuana*. It has not been observed in the other species.

IV. Rough-barked Bloodwoods

The phloem of the rough-barked species shows a different fundamental pattern from that of the smooth-barked, but there is no feature on which the Corymbosae can be distinguished from the Corymbosae-peltatae. The fibre bundles are less extended tangentially and more nearly oval in shape, and the parenchyma is more conspicuous in the inner phloem, but usually without very marked or very regular expansion in the outer phloem. The most conspicuous feature of these species is the enormous fibre enlargement which occurs in the phloem of the older stems and branches. The very young twigs have a structure that is very little different from that of the deciduous species, and it is only as the tree gets older that the characteristic phloem structure begins to appear. This development has already been described for *E. gummifera* (Chattaway 1953).

The rhytidome of the rough-barked species is very variable; it may be of the stringybark type (Chattaway 1953), with marked radial expansion of the rhytidome parenchyma (Plate 3, Fig. 4), or there may be little expansion (Plate 3, Fig. 2); in the latter case the rhytidome pattern is very similar to that of the outer phloem.

The size of the largest fibres of the rough-barked species is shown in Table 1. Each fibre bundle in these species also contains a number of small fibres, the number varying in different samples. These are of a fairly uniform diameter of 30-45 μ. In most of these species the large fibres are very numerous, several occurring in every fibre bundle, but their size and frequency vary from sample to sample. It seems likely that such variation is affected by the age of the tree and the height above ground level at which the material was taken. Samples known to be from branch material or stems of small size have always contained fewer and smaller enlarged fibres.

Enlarged fibres have not been observed in the two rough-barked species *E. ficifolia* and *E. jacobsiana*. The pattern of fibre bundle arrangement in *E.*

ficifolia is similar to that in the other rough-barked bloodwoods, but the fibres are of small cross-sectional diameter (Plate 2. Fig. 6). No expanded fibres have been

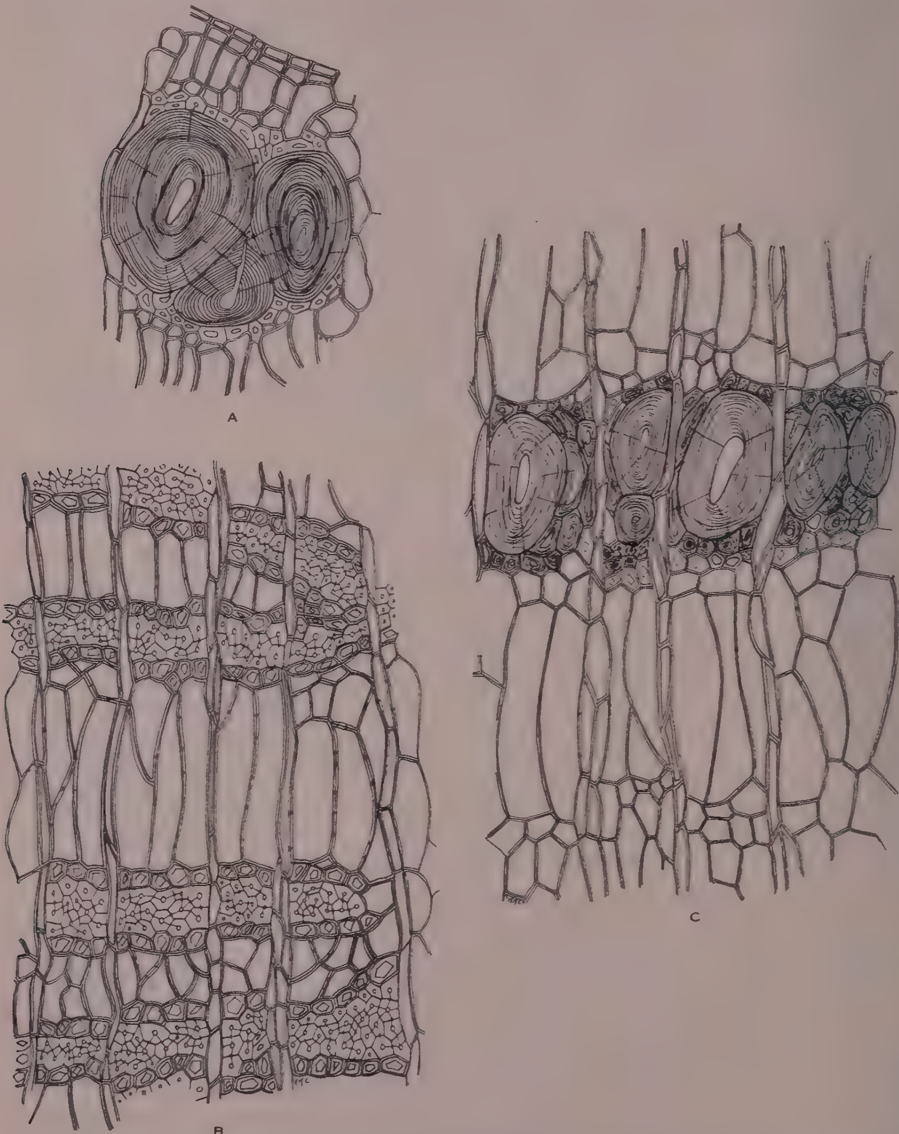

Fig. 1.—*E. gummifera* (Gaertn.) Hochr. (*A*), *E. maculata* Hook. (*B*), and the hybrid between them, *E. nowraensis* Maiden (*C*). × 225.

observed in six samples from different trees of this species. In *E. calophylla* large fibres have always been present in some bundles of all 10 samples of trees from the type locality in Western Australia, in one sample from the Northern Territory,

and in one from the Melbourne Botanic Gardens. Three other cultivated trees have the phloem structure of *E. ficifolia*. It seems likely that most of the cultivated trees are hybrids between *E. calophylla* and *E. ficifolia* and represent varying intergrades in structure between the two parents.

A few local patches of radially elongated phelloderm were observed in two samples of *E. ficifolia*.

The other species with a different bark structure is *E. jacobsiana*, of which only one specimen was available. In this species the bark is different in detail from any other of the bloodwoods examined, bearing only a slight resemblance to the fundamental pattern of the smooth-barked species and lacking the expanded fibres that are characteristic of most of the rough-barked species. However, the affinities of this species are not very certain, and it may be incorrectly placed in this series. Blakely (1934) says of it that "It is the most striking species of the very unique series Corymbosae and differs from its allies in the *Angophora*-like reticulately veined leaves, in the velvety tomentum on the lower surface of the juvenile leaves, in the fibrous nature of its bark and in the dark brown timber. Were it not for its typical Corymbose fruits, which resemble those of *E. trachyphloia*, it could easily be mistaken in the Herbarium for *Angophora bakeri*, a beautiful New South Wales tree. It has no very close affinities in its sub-series." The bark of *E. jacobsiana* differs not only from the bloodwoods but also from the *Angophora* species examined (Plate 4, Figs. 2 and 3). The bundles of phloem fibres form long tangential bands which appear as concentric bands, and the parenchyma is less abundant than in the bloodwoods; the fibres are small and consistently have a greater tangential than radial character; successive periderms form in almost every parenchyma row. It is without any very distinctive features so that it is impossible to suggest affinities from the bark structure.

V. Other Large-fibred Species

The bark of the Miniatae must be considered at the same time as that of the bloodwoods (see Table 2), as the details of structure are so similar. Only one sample of each species was available and, although the fibres of *E. miniata* A. Cunn. are smaller than the general range of large bloodwood fibres, the enlargement is sufficiently great and the pattern of the phloem sufficiently marked to show the close similarity. Maiden (1903-33) writes: "In its bark *E. miniata* displays considerable affinity to the Corymbosae", and of *E. phoenicea* F. Muell. he says it has affinities with *E. miniata*, from which it is difficult to distinguish it, and "with *E. corymbosa*, the urceolate fruits suggest an affinity, while the barks of both *E. phoenicea* and *E. miniata* undoubtedly display affinities to that of *E. corymbosa* and other members of the bloodwood group". *E. corymbosa* Sm. is a synonym for *E. gummifera* (Gaertn.) Hochr.

The other large-fibred species are further removed in relationship from the bloodwoods, but as they are unusual in possessing this feature, and number only 13 out of 261 species examined, they may be worthy of mention. The measurements of the largest fibres for these species are given in Table 2.

Outlines of bloodwood fibres, both large and small, are shown in Figure 2, and outlines of some other large-fibred species in Figure 3. The distortion which is so noticeable a feature of the large bloodwood fibres seems to be merely a factor resulting from their development among the cells of other differentiating tissues

TABLE 2

DIAMETERS OF OTHER LARGE-FIBRED EUCALYPTS

Species	No. of Samples	Average Diameter (μ) of Enlarged Fibres	
		Radial	Tangential
II. MINIATAE			
miniata	2	120	95
phoenicea	1	114	75
IX. SUBCORNUTAE			
redunca	3	95	60
wandoo	2	95	56
XI. DUMOSAE			
accedens	4	123	75
XV. EXSERTAE			
parramattensis	1	114	57
XXII. PANICULATAE			
cloeziana	11	133	95
XXX. FRAXINALES			
planchoniana	11	114	60
XXXII. PIPERITALES			
congener	1	65	53
linearis	2	103	61
risdoni	2	100	76
tasmanica	2	91	61
XXXIII. PSATHYROXYLA			
haemastoma	3	133	76
micrantha	9	91	57
rossii	9	103	68

among which they are forced by their enlargement. It can be seen to a modified extent in *E. accedens*, one of the larger-fibred species shown in Figure 2.

In the Psathyroxyla the large-fibred bundles tend to be few in number and are dispersed among typical bundles of small fibres.

VI. DISCUSSION

The classification used in this paper is that of Blakely (1934), and is the one in general use for the whole genus *Eucalyptus*. Recently, however, S. T. Blake (1953) has reviewed the northern Australian species of *Eucalyptus* and has suggested important changes in their nomenclature and classification.

Maiden, in his "Critical Revision of the Genus *Eucalyptus*" (1903-33), subdivided the bloodwoods into two series, the Corymbosae and the Corymbosae-peltatae, which he distinguished from one another by the shape of the juvenile leaves; within each series the species could be further divided and Maiden suggested that what he called the "angophoroid" species of the Corymbosae (*aspera*, *clavigera*, *grandiflora*, etc.) were more closely allied to one another and to the genus *Angophora* than to the

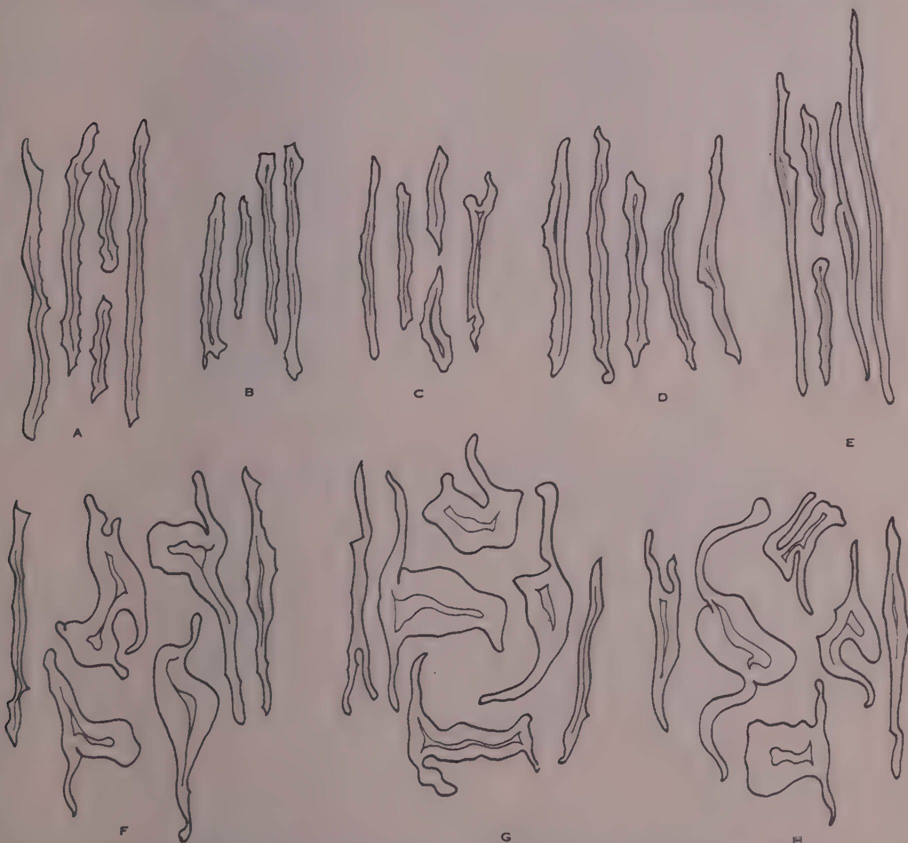

Fig. 2.—Outline drawings of bloodwood fibres. × 225. *A*, *E. grandifolia* R. Br.; *B*, *E. gilbertensis* (Maiden & Blakely) S. T. Blake; *C*, *E. maculata* Hook.; *D*, *E. citriodora* Hook.; *E*, *E. confertiflora* F. Muell.; *F*, *E. setosa* Schauer; *G*, *E. polycarpa* F. Muell.; *H*, *E. dichromophloia* F. Muell.

rest of the Corymbosae. He further considered that *E. citriodora* and *maculata* (which he thought to be varieties of one species, though now generally separated), were more like the *Angophora* species than like the rest of the Corymbosae-peltatae.

As a result of intensive work on many of these species Blake (1953) suggests that the Clavigerae (a series originally proposed by Maiden, but later discarded in favour of the Corymbosae-non-peltatae) should be reintroduced, to contain *E. aspera*, *clavigera*, *confertiflora*, *gilbertensis*, *grandifolia*, *papuana*, and *tessellaris*.

This is a series which is well founded, not only on the morphology, but also on the anatomy of the bark.

Such a rearrangement, however, leaves four small-fibred species among the otherwise homogeneous large-fibred, rough-barked species. They are *E. citriodora*, *jacobsiana*, *maculata*, and *torrelliana*. Blake does not deal with *E. citriodora* and

Fig. 3.—Outline drawings of large fibres of other *Eucalyptus* species. × 225. *A*, *E. accedens* W. V. Fitzgerald; *B*, *E. rossii* Baker & Smith; *C*, *E. planchoniana* F. Muell.

maculata in detail, as their distribution does not lie within the scope of his work, but he mentions them as departing somewhat from the general trend of the Corymbosae as defined in his paper.

E. torrelliana is a semi-deciduous species, and would seem, from the bark anatomy, to have more in common with the Clavigerae than with the rough-barked species (Plate 1, Fig. 5).

Judged from the one bark specimen available for examination, *E. jacobsiana* does not seem to fit well into either of the bloodwood series when its bark anatomy

alone is considered. As already mentioned Blakely did not consider that its affinities were with the bloodwoods, although he classified it with them. Unfortunately only dry bark was available for examination, which increased the difficulty of obtaining good sections, and the features observed are not distinctive enough for alternative suggestions to be made (Plate 4, Fig. 2).

Maiden (1903-33) suggested an affinity between the bloodwoods and *Angophora* species. The bark of four species of *Angophora* was examined, as follows: *A. bakeri* E. Cuthbert Hall (4); *A. costata* (Gaertn.) Britt. (2); *A. floribunda* (Sm.) Domin (1); *A. lanceolata* Cav. (1). In these there is no noticeable difference in phloem structure between the rough- and the smooth-barked species (Plate 4, Figs. 3-5). The structure is very similar to that of the small-fibred bloodwoods and to *E. ficifolia* among the rough-barked species; no enlarged fibres were observed in any of the material examined. In all species there is considerable expansion of the parenchyma in the outer phloem, the pattern of the smooth-barked species being very similar to that of *E. citriodora* (Plate 4, Figs. 1 and 4); in the rough-barked species there is little further expansion in the rhytidome, which is very similar in general pattern to that of *E. ficifolia*. It would appear as if any relationship must be through the small-fibred bloodwoods, and that the enormous expansion of the rough-barked ones represents an independent line of evolution.

VII. Acknowledgments

The author wishes to thank all who have assisted by advice and by collection of material, the cutting of sections, and the taking of photographs.

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Explanation of Plates 1-4

Plate 1

Fig. 1.—*E. aspera* F. Muell. Cross section of outer phloem. × 47.

Fig. 2.—*E. papuana* F. Muell. Cross section of phloem showing small fibres and crystalliferous parenchyma. × 180.

Fig. 3.—*E. papuana* F. Muell. Showing sclerosed parenchyma with bordered pits. × 96.

Fig. 4.—*E. aspera* F. Muell. Cross section of outer phloem showing diversion of ray direction resulting from parenchyma expansion. × 109.

Fig. 5.—*E. torrelliana* F. Muell. Cross section of outer phloem showing diversion of ray direction resulting from parenchyma expansion. × 94.

Plate 2

Figs. 1 and 2.—*E. maculata* Hook. Cross sections of expanded parenchyma in outer phloem, showing bordered pits. × 180.

Fig. 3. *E. maculata* Hook. Cross section of outer phloem showing expanded parenchyma. × 47.

Fig. 4.—*E. confertiflora* F. Muell. Cross section of outer phloem, showing radially elongated phelloderm. × 47.

Figs. 5-8.—Cross sections of phloem fibres. × 103. 5, *E. abergiana* F. Muell. 6, *E. ficifolia* F. Muell. 7, *E. watsoniana* F. Muell. 8, *E. dichromophloia* F. Muell.

PLATE 3

Fig. 1.—*E. setosa* Schauer. Cross section of rhytidome, showing expanded parenchyma. × 65.

Fig. 2.—*E. bloxomei* Maiden. Cross section of rhytidome, no expansion of parenchyma. × 65.

Figs. 3-11.—Cross sections of phloem fibres. × 103. 3, *E. cloeziana* F. Muell.; 4, *E. miniata* A. Cunn.; 5, *E. phoenicea* F. Muell.; 6, *E. redunca* Schauer; 7, *E. accedens* W. V. Fitz.; 8, *E. micrantha* DC.; 9, *E. phoenicea* F. Muell.; 10, *E. linearis* Dehn.; 11, *E. risdoni* Hook. f.

PLATE 4

Fig. 1.—*E. citriodora* Hook. Outer phloem. × 47.

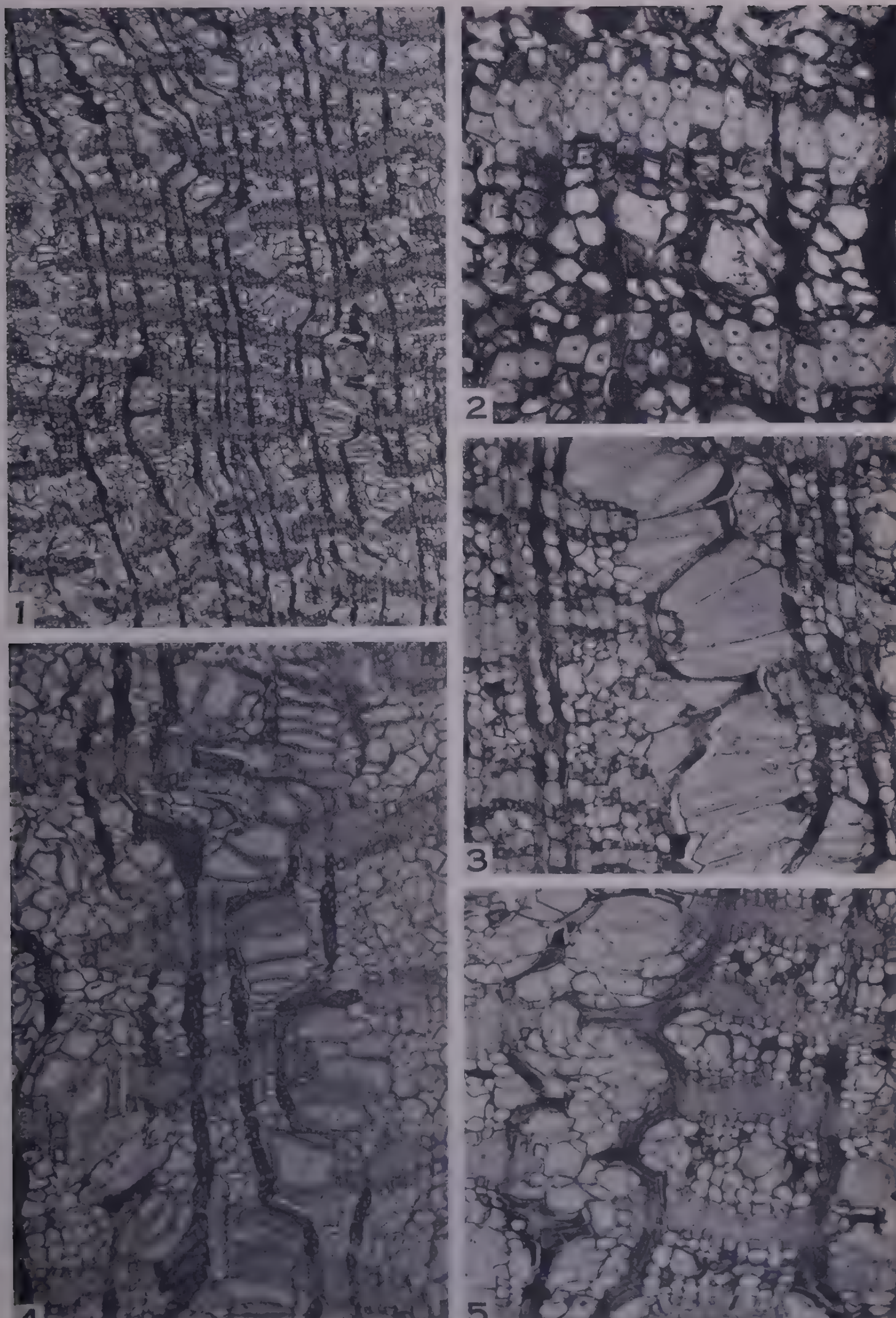
Fig. 2.—*E. jacobsiana* Blakely. Inner phloem. × 150.

Fig. 3.—*Angophora bakeri* E. Cuthbert Hall. Inner phloem. × 150.

Fig. 4.—*Angophora lanceolata* Cav. Outer phloem. × 47.

Fig. 5.—*Angophora costata* (Gaertn.) Britt. Inner phloem. × 47.

THE ANATOMY OF BARK. III



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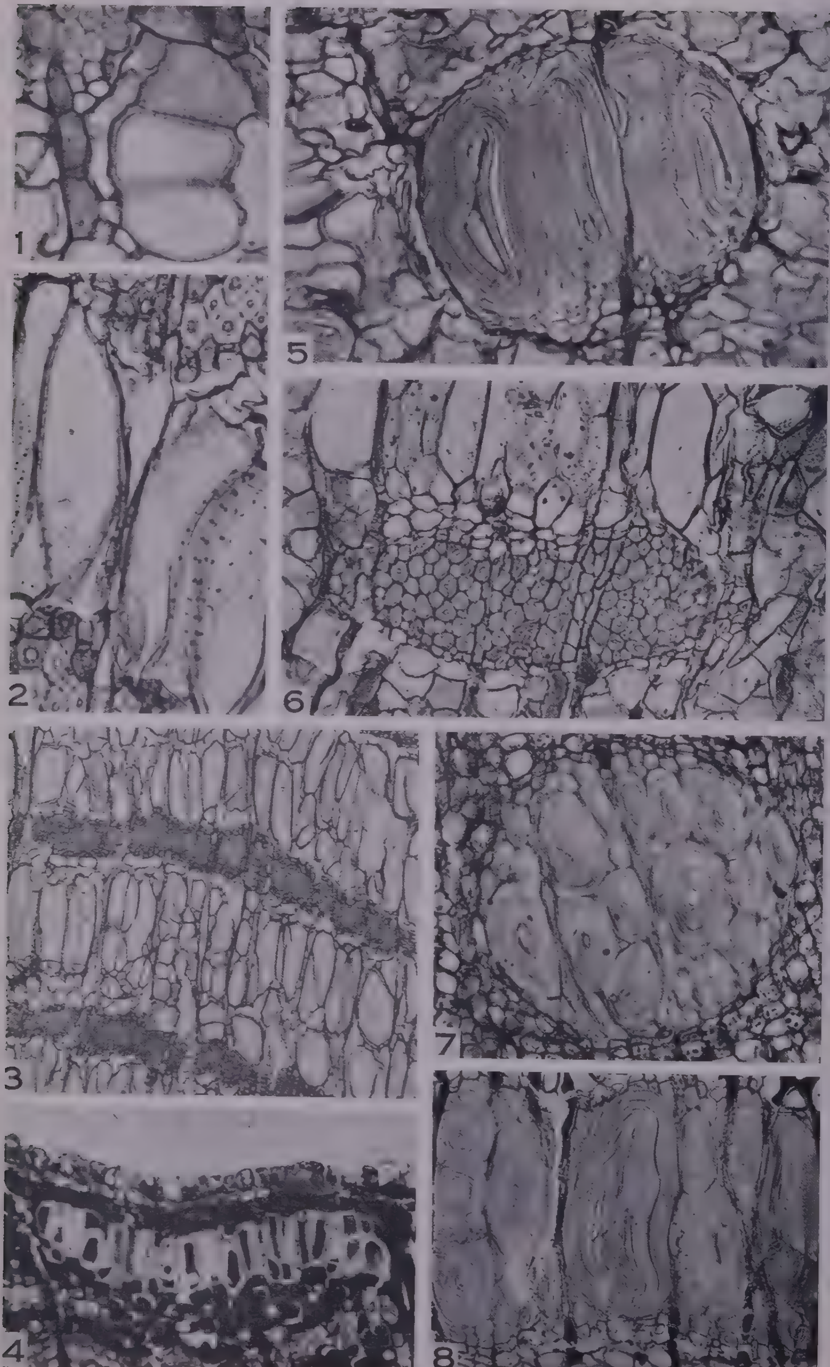
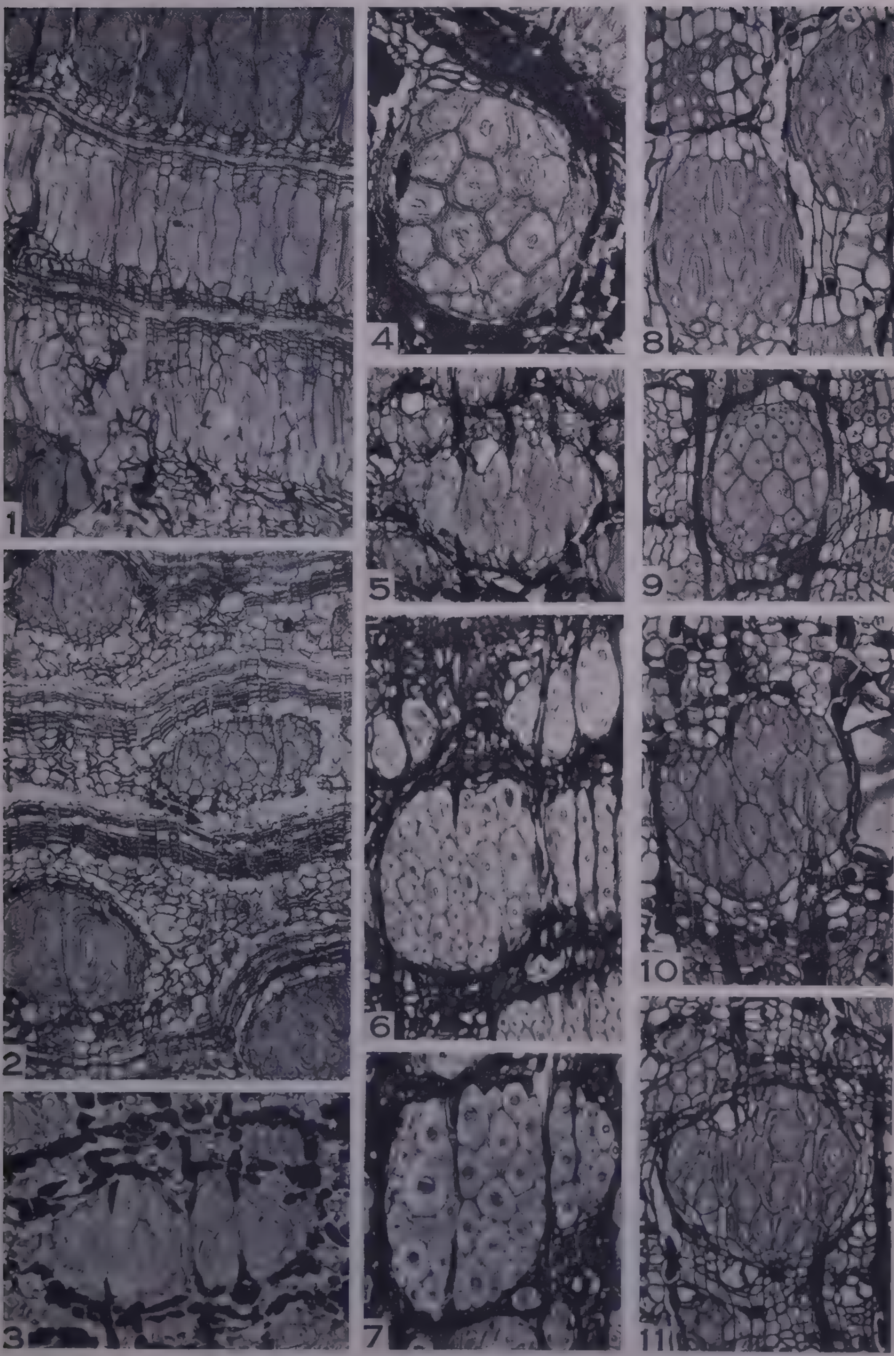
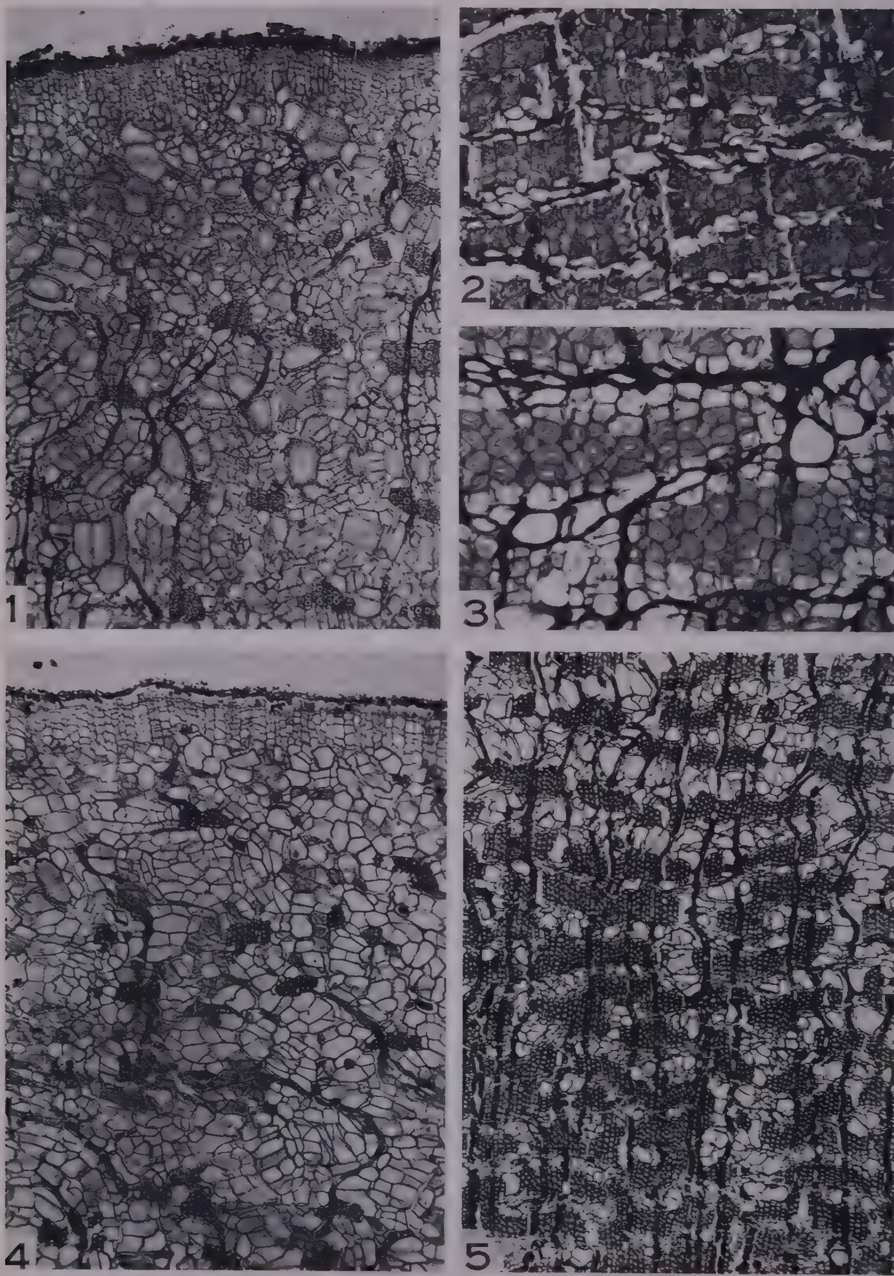


THE ANATOMY OF BARK. III



THE ANATOMY OF BARK. III



THE ANATOMY OF BARK

IV. RADIALLY ELONGATED CELLS IN THE PHELLODERM OF SPECIES OF EUCALYPTUS

By M. Margaret Chattaway*

[*Manuscript received November 24, 1954*]

Summary

The occurrence of a palisade of radially elongated cells, sometimes heavily sclerosed, in the phelloderm of certain species of *Eucalyptus* is described. These cells have been observed in 71 out of 272 species examined. They vary greatly in degree of development both between different species and, in some instances, between different samples of the same species.

The extreme variation observed in this feature is discussed with special reference to the occurrence of interspecific hybridization within the genus.

I. Introduction

In earlier papers on the structure of eucalypt bark (Chattaway 1952, 1953*a*, 1953*b*) reference has been made to the radial elongation that takes place in the inner rows of the phelloderm to produce, in the most extreme instances, bands of strongly cohesive cells, which become air-filled in the dry rhytidome and form a conspicuous feature, sometimes even visible to the naked eye, of cross sections of the bark of some eucalypt species. This appears to be the extreme form of development of a feature which may appear in other species of *Eucalyptus* as a layer of heavily sclerosed cells which form a palisade developing continuously or sporadically in the phelloderm (Fig. 1*A-B*). In its least conspicuous form it may appear as a group of thicker-walled cells, sometimes with little radial elongation (Fig. 1*C*). Such variation can even be found in different samples of the same species (Figs. 2 and 3), and somewhat less variation occasionally in samples from different parts of the same tree.

Radially elongated or sclerosed phelloderm cells have been observed in only 71 out of the 272 eucalypt species examined, occurring more commonly in some groups than in others, but rarely consistently in any one group of closely related species. In this it must be considered different from the much enlarged fibres of the bloodwoods (Chattaway 1953*a*, 1953*b*, 1955*b*) or the oil glands which are present in the outer phloem of a number of closely related groups (Chattaway 1953*a*, 1955*a*). It is difficult to explain its sporadic occurrence throughout the whole species range of the genus, but a clue to this may lie in the past, in a history of generations of hybridization.

II. Material

The species listed in Table 1 show some degree of phelloderm development, having radially elongated cells that either form a more or less continuous layer under the periderm or occur in sporadic patches. The table includes also the

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approximate length of the cells radially, the number of specimens of each species examined, and the degree of variability within the species. The number in brackets following the group is the number of species available for examination.

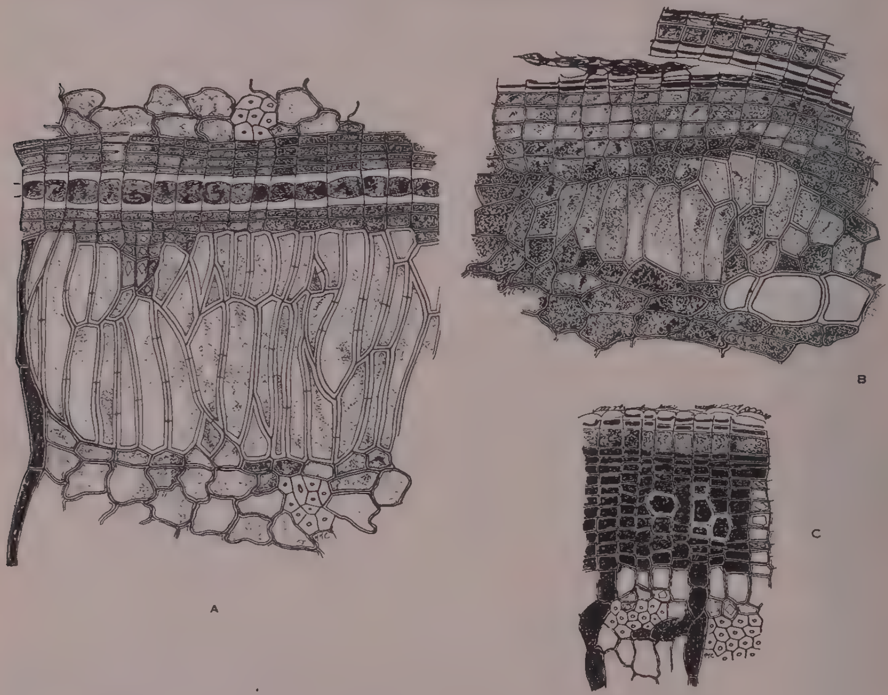

Fig. 1.—Variation in development of phelloderm. *A*, *E. deanei* Maiden; *B*, *E. robusta* Sm.; *C*, *E. dealbata* A. Cunn. × 225.

Radially elongated phelloderm cells have not been observed in the following series (the number in brackets is the number of species examined from each series):

Eudesmieae (6)	Miniatae (2)	Tetrapterae (1)
Obliquae (5)	Cornutae (10)	Sub-cornutae (3)
Microcorythae (1)	Decurvae (1)	Elongatae (1)
Argyrophyllae (2)	Paniculatae (5)	Diversiformae (2)
Occidentales (2)	Ochroxylon (1)	White mahoganies (3)
Steatoxylon (1)	Myrtiformes (1)	Fruiticosae (1)
Sub-buxeales (6)	Siderophloiae (10)	Aridae (3)
Eremophilae (1)	Leptopodae (5)	Contortae (1)
Quadricostatae (2)	Xylocarpae (1)	

No material of the Anisomeleae was available for examination. The classification used throughout this study is that of Blakely (1934).

III. Occurrence and Development

As soon as the tangential expansion of a young stem exceeds the capacity for tangential stretching and division of the epidermal cells, periderms start to

TABLE I

RADIALLY ELONGATED CELLS IN EUCALYPTUS SPP.

Numbers in brackets are numbers of species examined

Species	No. of Samples Examined	Radially Elongated Cells			Max. Rad. Dia. (μ)
		Well Developed	Poorly Developed	Absent	
IV. CORYMBOSAE (14)					
aspera F. Muell.	1	—	1	—	76
confertiflora F. Muell.	5	2	1	2	106
papuana F. Muell.	8	1	4	3	114
V. CORYMBOSAE-PELTATAE (16)					
ficifolia F. Muell.	6	3	2	1	210
VI. TRANSVERSAE (18)					
botryoides Sm.	9	9	—	—	320
canaliculata Maiden	2	1	1	—	171
cosmophylla F. Muell.	5	5	—	—	152
deanei Maiden	10	9	1	—	210
diversicolor F. Muell.	2	—	2	—	114
grandis (Hill) Maiden	7	4	3	—	100
jacksoni Maiden	3	3	—	—	170
longifolia Link & Otto	13	11	2	—	247
major Blakely	6	2	—	4	123
pellita F. Muell.	25	5	2	18	200
propinqua Deane & Maiden	2	1	1	—	123
punctata DC.	11	7	2	2	160
robusta Sm.	11	—	2	9	95
saligna Sm.	11	11	—	—	214
shiressii Maiden & Blakely	1	1	—	—	123
XI. DUMOSAE (16)					
clelandi Maiden	2	—	1	1	95
le souefi Maiden	3	—	1	2	65
XV. EXSERTAE (12)					
bancrofti Maiden	2	1	1	—	100
blakelyi A. Cunn.	30	7	10	13	210
camaldulensis Dehn.	81	27	21	33	247
dealbata A. Cunn.	10	3	2	5	114
dwyeri Maiden & Blakely	8	1	2	5	85
rudis Endl.	3	—	2	1	57
seeana Maiden	4	3	—	1	160
tereticornis Sm.	12	—	2	10	75
XVI. SUBEXSERTAE (6)					
alba Reinw.	7	6	1	—	133
studleyensis Maiden	4	—	1	3	60

TABLE 1 (*Continued*)

Numbers in brackets are numbers of species examined

Species	No. of Samples Examined	Radially Elongated Cells			Max. Rad. Dia. (μ)
		Well Developed	Poorly Developed	Absent	
XVII. MICROCARPAE (4)					
maculosa R. T. Baker	17	14	3	—	190
XVIII. GLOBULARES (21)					
dalrympleana Maiden	6	6	—	—	170
dunnii Maiden	1	—	1	—	75
goniocalyx F. Muell.	40	4	14	22	114
mannifera (A. Cunn. Herb.) Mudie	3	2	—	1	90
megacarpa F. Muell.	3	1	1	1	114
perriniana (F. Muell.) Rodway	4	—	2	2	57
rubida Deane & Maiden	19	17	2	—	210
unialata Baker & Smith	2	—	2	—	114
XIX. SEMIUNICOLORES (4)					
johnstoni Maiden	3	1	—	2	190
XX. VIMINALES (7)					
huberiana Naudin	6	1	2	3	95
viminalis Labill.	68	27	17	24	160
XXVI. PSEUDO-STRINGYBARKS (2)					
pilularis Sm.	9	8	—	1	228
XXIX. PACHYPHLOIAE (17)					
baxteri (Benth.) Maiden & Blakely	9	4	2	3	171
fastigata Deane & Maiden	7	4	3	—	262
laevopinea R. T. Baker	10	1	—	9	133
macrorrhyncha F. Muell.	9	—	1	8	76
obliqua L'Herit.	20	20	—	—	475
regnans F. Muell.	30	19	4	7	190
wilkinsoniana R. T. Baker	4	—	1	3	80
XXX. FRAXINALES (7)					
consideniana Maiden	5	2	3	—	95
gigantea Hook. f.	7	7	—	—	343
planchoniana F. Muell.	10	7	3	—	171
XXXI. LONGITUDINALES (5)					
pauciflora Sieb.	13	10	3	—	380

TABLE 1 (*Continued*)

Numbers in brackets are numbers of species examined

Species	No. of Samples Examined	Radially Elongated Cells			Max. Rad. Dia. (μ)
		Well Developed	Poorly Developed	Absent	
XXXII. PIPERITALES (14)					
andrewsi Maiden	6	2	3	1	133
campanulata R. T. Baker	7	2	5	—	209
linearis Dehn.	3	—	2	1	114
piperita Sm.	5	5	—	—	235
salicifolia (Sol) Cav.	3	—	1	2	76
urceolaris Maiden & Blakely	2	2	—	—	262
XXXIII. PSATHYROXYLA (3)					
haemastoma Smith	3	2	1	—	171
micrantha DC.	9	9	—	—	247
rossii Baker & Smith	8	8	—	—	247
XXXVII. BUXEALES (15)					
bosistoana F. Muell.	8	3	3	2	190
XXXIX. MELLIODORAE (1)					
melliodora A. Cunn.	26	5	9	12	171
XL. HETEROPHLOIAE (5)					
baueriana F. Muell.	3	2	—	1	262
conica Deane & Maiden	1	—	1	—	76
polyanthemos Schauer	20	11	8	1	228
rudderi Maiden	1	1	—	—	152
XLII. SUBULATAE (6)					
squamosa Deane & Maiden.	1	1	—	—	304

form and to cut deep into the cortex and outer phloem. The meristematic layer of the periderm may produce one to many rows of phelloderm, the number varying not only from species to species, but within a species from sample to sample, and sometimes even from point to point in a single sample. In some species the cells of one or more layers of the phelloderm appear to retain a capacity for growth which is not possessed by the other cells, and quickly enlarge to many times their previous size, the increase usually being far greater radially than tangentially or vertically. Sometimes the growth is not only an expansion, but also involves a great deposition of wall substance.

Figures illustrating stages in development in *Eucalyptus obliqua* were shown in a previous paper (Chattaway 1953*a*). The nuclei and protoplasm are a conspicuous feature of the enlarging cells, which usually contain less tannin than their neighbours.

E. obliqua appears to be the species in which the radial elongation of the phelloderm is most pronounced and most constant. The cells are by far the largest observed and may enlarge so much that they can be seen with the naked eye in old bark, where their air-filled condition helps to make them conspicuous. Their development is so constant that they have been found in every periderm in the thick bark of old trees and were well developed in every periderm of every section of the 20 samples examined. They begin to develop in young twigs, being initiated when the first signs of rough bark appear on the young twigs.

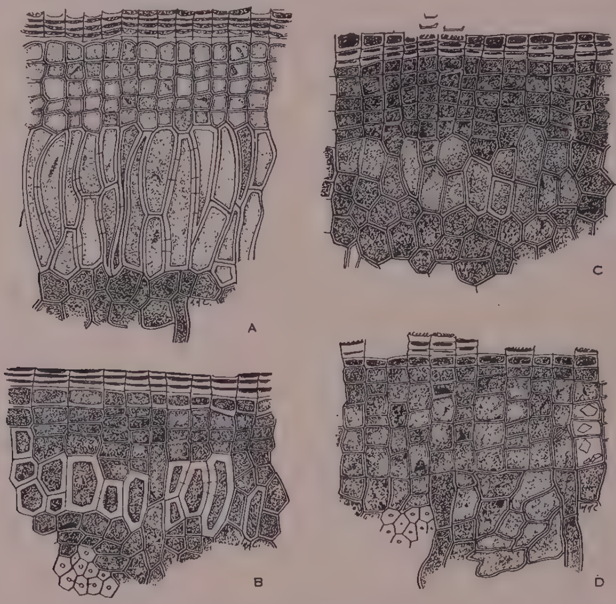

Fig. 2.—*E. viminalis* Labill. Variation in development of phelloderm in different trees. × 225.

In *E. regnans* radially elongated phelloderm cells do not develop so early in the young tree. A survey of 15 young trees has already been reported (Chattaway 1953*a*). The development of radially elongated cells varied from tree to tree; they were fully developed only in the larger trees and absent from the smaller, suppressed ones. These trees were all the same age (about 6-8 years) and were growing close together under the same conditions of soil and climate. Fully developed layers of radially elongated cells have been observed in all full-grown older trees of *E. regnans*.

Extreme examples of variability have been found in *E. viminalis* (Fig. 2) and *E. camaldulensis* (Fig. 3), of which 68 and 81 trees respectively have been examined.

It was originally thought that *E. viminalis* and *E. rubida* could be distinguished by the presence or absence of radially elongated cells, but examination of numerous samples of the former showed this to be erroneous. Although all of 19 samples of *E. rubida* showed radially elongated cells (well developed in all but two), *E. viminalis* proved to be a very variable species. This holds not only for the

bark, which varied from a few millimetres to about $1\frac{1}{2}$ in. in thickness and from smooth to rough, but also for the wood. Radially elongated phelloderm cells were well developed in 27 samples, absent from 24, and poorly developed or sporadic in 17. Material collected along creek beds in Victoria from trees which appeared to be of similar size and age showed all degrees of development in trees of the same stand. No consistent differences in external appearance of the trunks of these trees was observed. This material was not growing near any *E. rubida*, but was alongside trees of *E. ovata* Labill.

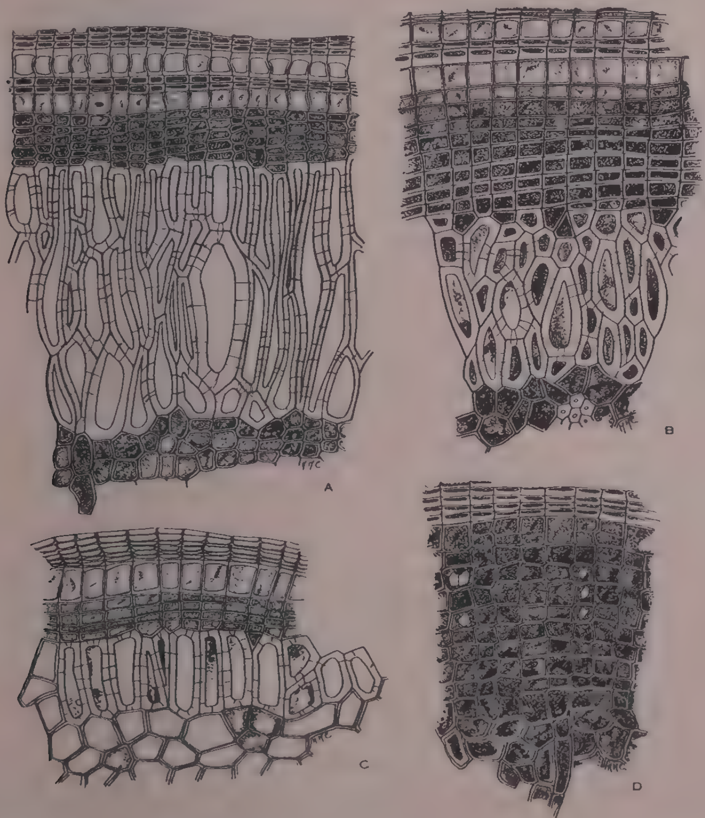

Fig. 3.—*E. camaldulensis* Dehn. Variation in development of phelloderm in different trees. × 225.

The variation in *E. camaldulensis* has been observed in material taken from approximately breast height in fully grown trees from a great variety of sites, ranging from Western Australia to New South Wales. Figure 3 shows the extremes of variation seen. On several trees it was possible to collect material specially for this investigation from many different points on a single tree, from north, south, east, and west sides, from different heights on the main trunk, and from branches.

The results showed that though there was considerable variation within a single tree it was never as great as that observed from tree to tree. In no case was there any correlation between the development of the phelloderm and the position in the tree or the geographical origin of material. Of 81 trees examined, 27 showed well-developed regular palisades of radially elongated phelloderm (Fig. 3*A*) or sporadic bands of sclerosed cells (Fig. 3*B*-*C*) and 33 were without any trace of radial elongation (Fig. 3*D*). Blocks for sectioning are always taken from the darker areas on the smooth trunks of the deciduous species, as these have been found to be the oldest, in order to obviate variation due to newly formed periderms. The bark varied in thickness and in appearance in different samples, but there appeared to be no correlation between these characters and the degree of phelloderm development.

IV. Discussion

The occurrence of radially elongated phelloderm presents anomalies of distribution; it occurs in many distantly related series of species and not in some that are more closely related; in some members of a series and not in others; and, above all, it shows extreme variability within a species.

It has not been possible to examine equally numerous samples of all species of *Eucalyptus*, and it is thus possible that if more material of some species were available the feature would be found to be present to some degree in more species than are listed here and that it might be found in all the species of a series in which it predominates, such as the Transversae. It occurs to some degree in 15 out of 18 species examined in the Transversae, being absent from *E. kirtoniana* F. Muell. and *E. pumila* Cambage, of each of which only one sample was available, and from nine samples of *E. resinifera* Sm.

Again, in the Exsertae radially elongated phelloderm was absent from only four of 12 species, of which samples were available as follows: *E. amplifolia* Naudin (4), *E. exserta* F. Muell. (3), *E. melanoxylon* Maiden (2), and *E. parramattensis* Hall (1). It is possible that in these species it might be observed to some degree if a larger number of specimens could be examined.

The most interesting aspect of this study is the extreme variability in regard to this feature from sample to sample of certain species. Recent work by taxonomic botanists has shown that hybridization between species is far commoner in the genus *Eucalyptus* than was previously thought. Pryor (1951) comments on the extreme variability of the genus which has caused earlier taxonomists to form a multiplicity of species out of a tree population consisting of various forms of different biological status. Many of these forms might under some circumstances be given the status of geographical or ecological subspecies, but unfortunately much of the variation encountered is not of the geographical kind. This has been noted above in *E. camaldulensis*, where examination of material from widely separated areas gave no correlation whatever for the various stages of development of radially elongated phelloderm. Both Pryor (1951) and Brett (1937) suggest that some of the variation encountered among *Eucalyptus* spp. could have been the result of active hybridization between species, with F_2 and back-cross segre-

gating swarms. Within the complex pattern of species in a eucalypt forest slight changes of altitude, soil, or climate may cause one species to give way to another, leaving pockets of trees of a single species which may show slight differences from the type due to their slightly different environment. Sometimes, where naturalists were numerous in the early days of settlement, these were given different species names, sometimes they were recognized as links in a varying chain of forms of a single species. Brett has suggested that such species are *polymorphic* and that the polymorphs have arisen by fixation, under varying conditions, of the segregates of previously existing hybrid swarms. Pryor's investigations of the hybrids of the Southern Tablelands of New South Wales support Brett's hypothesis. This concept of hybrid polymorphs appears to offer a possible explanation of the variation described in this paper, and is supported by evidence which is gradually being accumulated from known hybrids and hybrid swarms (Chattaway 1953*b*).

It is hoped to describe the bark of some of these hybrids in a later paper. In connexion with the present problem it is sufficient to say that many of them show the type of variation described here, and that it appears likely that material collected as examples of a certain species may be unsuspected polymorphs resulting from some past hybridization.

V. Acknowledgments

The author wishes to acknowledge her indebtedness to the many forest officers and others who have assisted by the collection and identification of material.

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CHROMOSOME NUMBERS AND POLLEN TYPES IN THE EPACRIDACEAE

By S. Smith-White*

[*Manuscript received October* 20, 1954]

Summary

Chromosome numbers are reported for 22 genera and 116 species of the Epacridaceae.

In the tribe Styphelieae, haploid numbers of 4, 6, 7, 8, 9, 10, 11, 12, and 14 occur. This numerical sequence does not represent a continuous series either of decrease or increase, but is built up from polyploid and aneuploid changes on base numbers of $x = 4$ and $x = 6$. Polyploid series on base 4 are found in *Cyathodes*, *Astroloma*, and *Leucopogon* § *Pleuranthus*, on base 6 in *Leucopogon* § *Perojoa*, and on base 7 in *Lissanthe*. Aneuploidy is also found within genera, but is generally more characteristic of particular genera.

In the Epacrideae, the usual haploid numbers are 13 and 12, and only one case of polyploidy is reported. Two species of *Sphenotoma* possess haploid numbers of $n = 6$ and $n = 7$ respectively. The base number for the Epacrideae is probably $x = 6$, and a relationship between the Epacrideae and the Styphelieae at the 6-chromosome level may be accepted. Any relationship between the Epacrideae and the Ericoideae at an amphidiploid level is denied.

With the exception of probable autotriploids in *Lissanthe montana*, meiosis is essentially regular throughout the family.

Tetrad-type pollen is characteristic of the Epacrideae. In the Styphelieae, the pollen is usually monad (*S*-type) and never truly single. Three variants in the pattern of pollen development occur in the tribe, modified monad (*S'*-type), full tetrad (*T*-type), and segregating tetrad (*A*-type). Variants in pollen development pattern are associated with aneuploidy.

The Epacridaceae must have had an ancient origin. Features of species distribution suggest that many may be post-Miocene in origin. Most of the genera must have been established in the early Tertiary, and the differentiation of the two tribes, the origin of the monad pattern of pollen development, and some fundamental changes in chromosome structure in the Styphelieae, permitting a period of chromosomal instability during their evolutionary diversification, must have been still more ancient.

I. Introduction

An earlier survey of chromosome numbers in the Epacridaceae (Smith-White 1948*a*) demonstrated two features of cytological interest. Chromosome numbers in the family are exceptionally variable. In the tribe Epacridaceae the usual haploid number is 13, suggesting a relationship with the South African Ericoideae. In the Styphelieae, there is a wide range of haploid numbers which appear to be derived from basic numbers of 4 or 6. Representatives of both the 4 and 6 series are found within the single genus *Leucopogon*. Some genera are aneuploid ($n = 7$, 9, 10) and in *Astroloma* aneuploid and polyploid numbers ($n = 7$, 12) occur. A view was expressed that certain genera of the Styphelieae are morphologically specialized but cytologically primitive, and that they could not be derivatives of the Epacrideae.

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The second feature of interest is the peculiar monad pattern of pollen development found in the Styphelieae. A third peculiar, if not unique, condition exists in the triploid species *Leucopogon juniperinus* (Smith-White 1948*b*, 1954*a*) in which permanence is maintained by complementary gametic elimination.

II. Materials and Methods

Table 1 presents a list of chromosome number determinations in the family. Counts have been made chiefly from aceto-lacmoid and aceto-orcein crushes of pollen mother cells and of leaf bud, ovary, and embryo tissue. Most of the new reports in the table are of Western Australian species, and some difficulty has been experienced in the naming of this material, particularly in the large genus *Leucopogon*.

III. Observations

(*a*) *Pollen Types*

In the Epacrideae the pollen is consistently matured in tetrads, a feature generally characteristic of the Ericales. In the Styphelieae, four different types of pollen and four patterns of pollen development occur (Table 1, column 8). The *Styphelia*-type monad pollen (*S*-type) consists of tetrads in each of which only one pollen grain develops (Smith-White 1948*a*). The pattern of development involves nuclear migration in the pollen mother cell after meiosis and the production of initially unequal microspores. A modification of this pattern of development (*S'*-type) is found in some species of *Leucopogon*; there is an absence of nuclear migration in the mother cell after meiosis, and the four microspores are initially of equal size. In subsequent development, one pollen grain outgrows the other three, and mature pollen is consistently monad. The third type of pollen consists of segregating tetrads, and individual mature tetrads may consist of any number, from 0 to 4, of viable pollen grains. The type has been designated "*A*-type" since it was first observed in *Astroloma*, but it is neither confined to nor characteristic of that genus. The fourth type of pollen is the "full tetrad" or *T*-type, similar to that of the Epacrideae. It is probable that true "single" pollen grains do not occur in the family.

(*b*) *Chromosome Numbers*

Tribe Styphelieae ($x = 4, 6, 7, 9, 11$)

Styphelia ($x = 4$).—Pollen *S*-type. In all species examined karyotypes are similar in number and in gross morphology. At mitotic metaphase (Figs. 1 and 2), the eight chromosomes are of approximately equal length (*c*. 3.0-4.0 μ) and have median centromeres. Centromeric constrictions are often very pronounced.

Astroloma ($x = 4, 7$).—Pollen *S*-type, *A*-type (two species). Most species resemble *Styphelia* in karyotype, but morphological differences between the chromosomes are present. In *A. xerophyllum* (Figs. 3 and 4) one pair of chromosomes are approximately twice as long as the others. In *A. prostratum* and *A. tectum* this difference is less pronounced, and in *A. pallidum*, *A. compactum*, and *A. epacridis* (Figs. 6, 7, and 10) all the chromosomes are of uniform length. Meiosis is regular, apart from a low incidence of bridges (Fig. 5) and other abnormalities.

TABLE 1

CHROMOSOME NUMBERS AND POLLEN TYPES IN THE EPACRIDACEAE

Genus and Species	Acc. No.	State	Localities	Chromosome Numbers		Pollen Type*	Remarks and References
				n	2*n*		
Tribe Styphelieae							
Styphelia § *Eustyphelia*							
S. longifolia R.Br.		N.S.W.	Gordon	4	8	*S*	Smith-White 1948*a*
S. laeta R.Br.		N.S.W.	Warrah, La Perouse	4	8	*S*	Figure 1
S. triflora Andr.		N.S.W.	National Park, Lane Cove	4	8	*S*	Smith-White 1948*a*
S. triflora var.		N.S.W.	Rylstone, Bathurst	4	8	*S*	
S. viridis Andr.		N.S.W.	La Perouse	4	8	*S*	Smith-White 1948*a*
S. tubiflora Sm.		N.S.W.	Audley, Kuring-gai	4	8	*S*	Smith-White 1948*a*
Styphelia § *Soleniscia*							
S. tenuiflora Lindl.	WA52/3	W.A.	Mt. Dale	4	8	*S*	Figure 2
Astroloma § *Stomarrhena*							
A. stomarrhena Sond.	WA52/31	W.A.	Hill R. district	16	*c.* 32	*S*	Figure 2
A. xerophyllum Sond.	WA52/12	W.A.	Gnangara	4	8	*S*	Figures 3-5
	WA52/44						
A. sp. (near *xerophyllum*)	WA52/28	W.A.	Hill R. district	4	8	—	Mature pollen not seen
A. prostratum R.Br.	WA52/47	W.A.	Morowa	4	8	*S*	Figure 6
A. tectum R.Br.	WA52/59	W.A.	Cranbrook-Borden	—	8	*S*	Figure 7
A. candolleanum Sond.	WA52/44		Mullewa-Geraldton				
	WA52/45	W.A.	Mullewa-Geraldton	4	8	S	
	WA50/56		Coorow				
A. microdonta F. Muell.	WA52/30	W.A.	Hill R. district	8	16	*S*	Figures 8, 9
A. pallidum R.Br.	WA50/100		Albany				
	WA52/2	W.A.	Mundaring	4	8	*S*	
	WA52/		Stirling Ra.				
A. compactum R.Br.	WA52/60	W.A.	Cranbrook-Borden	—	8	*S*	
A. humifusum R.Br.		N.S.W.	Audley, Berowra	—	24	*S*	
A. epacridis DC.	WA52/62	W.A.	Chester Pass	—	8	*S*	Figure 10
A. microcalyx Sond.	WA52/81	W.A.	Gleneagle, King's Park	4	8	*S*	
A. ciliatum Druce	WA50/101		Albany				
	WA52/33	W.A.	Jurien Bay Rd.	4	8	*S*	

* Key to pollen type abbreviations: *S*, *Styphelia*-type monads; *S′*, modified *Styphelia*-type monads; *T*, full tetrad pollen; *A*, *Astroloma*-type segregating tetrad pollen.

TABLE 1 (*Continued*)

Genus and Species	Acc. No.	State	Localities	Chromosome Numbers		Pollen Type	Remarks and References
				n	$2n$		
Tribe Styphelieae (*Continued*)							
A. sp. (near *tectum*)	WA52/	W.A.	Kalgan R.	4	8	*S*	
A. sp (?)	WA52/13	W.A.	Gnangara	6	12	—	Figures 12, 13. Mature flowers not seen
Astroloma § *Pentataphrus*							
A. conostephioides F. Muell	SA52/5	S.A.	Streaky Bay, Elliston	7	14	*A*	Figure 14
Astroloma § *Stenanthera*							
A. pinifolium Benth.		N.S.W.	Audley, Warrah, Evans Head	7	14	*A*	Smith-White 1948*a* Figures 15, 16
Conostephium							
C. pendulum Benth.	WA50/6	W.A.	King's Park	—	16	*S*	
C. preissii Sond.	WA52/	W.A.	King's Park, Moore R.	—	16	*S*	
Melichrus							
M. rotatus R.Br.		N.S.W.	Lane Cove	8	16	*S*	Smith-White 1948*a*
M. urceolatus R.Br.		N.S.W.	Albury, Rylstone	8	16	*S*	Smith-White 1948*a*
Pentachondra							
P. pumila R.Br.		N.S.W.	Kosciusko	—	28	*T*	
Trochocarpa							
T. laurina R.Br.		N.S.W.	Hacking R.	10	—	*T*	Smith-White 1948*a*
Cyathodes							
C. glauca Labill.		Tas.	National Park	—	24	—	Figure 17. Pollen not seen
C. adscendens Hook.		Tas.	National Park	—	18	*T*	Figure 18
C. divaricata Hook.		Tas.	National Park	—	24	Nil	Anthers sterile
C. parviflora R.Br.		Tas.	National Park, Mt. Wellington		20	Nil	Anthers sterile
C. parviflora R.Br.		Tas.	Great Lake	—	—	*S*	
C. tamaeiameae Cham.		Oceanic		—	—	*T*	Cf. Erdtman 1945
C. douglasii A. Gray		Oceanic		—	-	*T*	Cf. Erdtman 1945

TABLE 1 (*Continued*)

Genus and Species	Acc. No.	State	Localities	Chromosome Numbers		Pollen Type	Remarks and References
				n	$2n$		
Tribe Styphelieae (*Continued*)							
Brachyloma							
B. preissii Sond.	WA52/16	W.A.	Bull's Creek	7	14	*A*	Figures 19-22
	WA52/35		Hill R. district				
	WA50/49		Cannington				
B. scortechinii F. Muell.		N.S.W.	Evans Head	9	—	*T′*	
B. daphnoides Benth.		N.S.W.	Lane Cove, Kuring-gai	9	18	*T*	Smith-White 1948*a*
Lissanthe							
L. sapida R.Br.		N.S.W.	Springwood	7	14	*T*	Smith-White 1948*a*
L. strigosa R.Br.		N.S.W.	Yagoona	7	14	*T*	Smith-White 1948*a*
L. montana R.Br.		N.S.W.	Kosciusko	14	28, 42	*T*	Figures 23-25
Leucopogon § *Perojoa*							
Series 1							
L. verticellatus R.Br.	WA52/21	W.A.	Busselton	11	22	*S′*	Figures 26-28
	WA52/57		Porongorups				
L. amplexicaulis R.Br.		N.S.W.	Audley, Kuring-gai	12	—	*S*	Smith-White 1948*a*
L. lanceolatus R.Br.		N.S.W.	Lane Cove, Bowral	24	—	*S*	Smith-White 1948*a*
Series 2							
L. richei R.Br.	WA52/17	W.A.	Flinders Bay	6	12	*S*	
	WA52/18						
L. australis R.Br.	WA52/	W.A.	Hill R. district				
	WA52/24		Busselton	*c.* 12	—	*S*	Figure 29
	WA52/65		Stirling Ra.	12	—	*S*	
L. capitellatus DC.	WA52/23	W.A.	Bunbury	11	—	*S′*	Figure 30
	WA52/39						

TABLE 1 (*Continued*)

Genus and Species	Acc. No.	State	Localities	Chromosome Numbers		Pollen Type	Remarks and References
				n	$2n$		
Tribe Styphelieae (*Continued*)							
L. revolutus R.Br.	WA52/56	W.A.	Porongorups	11	—	S'	Figures 31-36
	WA52/148		Nannup				
L. corifolius Endl. (?)	WA52/50	W.A.	Morowa	6	12	—	
				11	22	—	Figure 37 Material mixed?
L. distans R.Br.	WA50/118	W.A.	Frenchman's Bay				
	WA52/53		Porongorups	11	—	S'	
L. gibbosus Stschegl.	WA52/64	W.A.		—	—	S'	
Series 3							
L. microphyllus R.Br.		N.S.W.	Kuring-gai, National Park	6	12	S	Smith-White 1948*a*
L. glabellus R.Br.	WA52/25	W.A.	Busselton	—	—	S'	
	WA52/54		Porongorups	—	—	T	
	WA52/55		Porongorups	11	—	S'	
	WA52/149		Nannup	—	—	S'	
	WA50/93		Albany	—	—	S'	
	WA50/95		Albany				
Series 7							
L. virgatus R.Br.*		N.S.W.	Albury	10	—	T	Smith-White 1948*a*
			Rylstone	6	—	S	
			Evans Head	—	—	S	
L. polymorphus Sond.	WA52/14	W.A.	Gnangara	—	—	S'	
L. assimilis R. Br.	WA50/96	W.A.	Albany	—	—	S	Or S'. Only mature pollen seen

* See footnote to *Leucopogon strongylocarpus*.

TABLE 1 (*Continued*)

Genus and Species	Acc. No.	State	Localities	Chromosome Numbers		Pollen Type	Remarks and References
				n	$2n$		
Tribe Styphelieae (*Continued*)							
L. oldfieldii Benth.	WA52/10	W.A.	Gin Gin	*c.* 12	—	—	
	WA52/36		North of Moore R.				
	WA52/37		North of Moore R.	11	—	*S′*	Figures 38-40
	WA52/58		Cranbrook				
	WA52/34		Gin Gin	*c.* 33	—	*S′*	
L. cuculatus R.Br.	WA52/9	W.A.	Moore R.	22	—	*S′*	Figure 41
L. sprengelioides Sond.	WA52/72	W.A.		—	—	*S′*	
Leucopogon § *Heteranthesis*							
L. hookeri Sond.	N53/	N.S.W.	Kosciusko	14	28	*T*	
Leucopogon § *Pleuranthus*							
Series 2							
L. muticus R.Br.		N.S.W.	Rylstone, Bulga Rd.	6	—	*S*	Figure 46
L. ericoides R.Br.		N.S.W.	Lane Cove, Audley	6	—	*S*	Smith-White 1948*a*
L. propinquus R.Br.	WA52/7	W.A.	Mundaring	4	8	*S*	Figures 42, 43
L. pendulus R.Br.	WA50/94	W.A.	Albany	—	8	*S*	
Series 3							
L. concinnus Benth.	WA52/67	W.A.		4	8	*S*	
L. margaroides R.Br.		N.S.W.	Evans Head	4	8	*S*	
L. flavescens Sond.	WA52/38	W.A.	Hill R. district	4	8	*S*	
L. esquamatus R.Br.		N.S.W.	Kuring-gai, Lane Cove	4	8	*S*	Smith-White 1948*a*
Series 4							
L. biflorus R.Br.		N.S.W.	Kosciusko, Cooma	8	16	*S*	Figure 45
L. setiger R.Br.		N.S.W.	Lane Cove, Audley	4	8	*S*	Smith-White 1948*a*
L. fraseri A. Cunn.		N.S.W.	Pidgeon House Ra.	4	8	*S*	Figure 44

TABLE 1 (*Continued*)

Genus and Species	Acc. No.	State	Localities	Chromosome Numbers		Pollen Type	Remarks and References
				n	2*n*		
Tribe Styphelieae (*Continued*)							
L. ovalifolius Sond.	WA52/68	W.A.	Manjimup, Nornalup	—	8	*S*	
L. oxycedrus Sond.	WA50/107	W.A.	Albany	—	8	*S*	
L. cuneifolius Stschegl.	WA52/49	W.A.	New Norcia, Morowa	—	8	*S*	
L. strictus Benth.	WA52/27	W.A.	Jurien Bay Rd.	—	8	*S*	
L. juniperinus R.Br.		N.S.W.	Sydney, Nowra, etc.	12/2	12	*S*	Triploid, Smith-White 1948*b*, 1954*a*
Series 5							
L. conostephioides DC.	WA52/11	W.A.	Gin Gin	—	12	*S*	
L. appressus R.Br.		N.S.W.	Kuring-gai	6	—	*S*	Smith-White 1948*a*
L. crassiflorus F. Muell.	WA52/29	W.A.	Hill R. district	6	—	*S*	Figure 47
L. strongylocarpus F. Muell.*	WA52/48	W.A.	Morowa-Mullewa	6	12	*S*	Figure 48
Acrotriche							
A. divaricata R.Br.		N.S.W.	Springwood	—	18	*T*	Smith-White 1948*a*
A. serrulata R.Br.		N.S.W.	Albury	9	—	*T*	Smith-White 1948*a*
A. ovalifolia R.Br.	WA52/22	W.A.	Busselton	—	18	*T*	Figures 49, 50
	WA52/66		Stirling Ra.				
A. fasciculiflora Benth.	SA52/8	S.A.	Blackwood	9	18	*A*	Figure 51
Monotoca							
M. elliptica R.Br.		N.S.W.	Narrabeen	12	24	*S*	Smith-White 1948*a*
M. scoparia R.Br.		N.S.W.	Gordon	12	—	*S*	Smith-White 1948*a*
			Newnes	—	—	—	
Tribe Epacrideae							
Epacris							
E. longiflora Cav.		N.S.W.	Audley, Kuring-gai	13	—	*T*	Smith-White 1948*a*
E. reclinata A. Cunn.		N.S.W.	Blackheath, Rylstone	13	—	*T*	

* Copeland (1954) has illustrated *T*-type pollen in *Leucopogon pedicellatus* and "single" pollen in *L. virgatus*.

TABLE 1 (*Continued*)

Genus and Species	Acc. No.	State	Localities	Chromosome Numbers		Pollen Type	Remarks and References
				n	$2n$		
Tribe Epacrideae (*Continued*)							
E. impressa Labill.		N.S.W.	Moruya	13	—	*T*	
E. rigida Sieb.		N.S.W.		13	—	*T*	
E. crassifolia R.Br.		N.S.W.	Springwood	13	—	*T*	Figure 52
E. obtusifolia Sm.		N.S.W.	King's Tableland	13	—	*T*	Smith-White 1948*a*
E. paludosa R.Br.		N.S.W.	King's Tableland	13	—	*T*	Smith-White 1948*a*
E. serpyllifolia R.Br.		N.S.W.	Kosciusko	13	—	*T*	
E. serpyllifolia		Tas.	National Park	26	—	*T*	
E. microphylla R.Br.		N.S.W.	Lane Cove, Kuring-gai	13	—	*T*	Smith-White 1948*a*
E. pulchella Cav.		N.S.W.	Lane Cove	13	—	*T*	Smith-White 1948*a*
Woollsia							
W. pungens (R.Br.) F. Muell.		N.S.W.	Kuring-gai	13	—	*T*	Smith-White 1948*a*
*Lysinema**							
L. ciliatum R.Br.	WA52/22 WA50/42	W.A.	Busselton	13	—	*T*	Figure 56
L. conspicuum R.Br.	WA	W.A.	Busselton	13	—	*T*	
Archeria							
A. sp.		Tas.	—	—	—	*T*	Cranwell 1942
Cosmelia							
C. rubra R.Br.	WA50/108	W.A.	Frenchman's Bay	13	—	*T*	
Sprengelia							
S. ponceletia F. Muell.		N.S.W.	Dee Why	12	—	*T*	Figure 55
S. ponceletoides Sond.		N.S.W.	Blackheath	—	—	*T*	
S. incarnata Sm.		N.S.W.	Kuring-gai	12	—	*T*	Smith-White 1948*a*

* Owing to an error of interpretation, the haploid numbers in *Lysinema* were given as n = 13 in lists forwarded to Dr. Wylie for inclusion in a new edition of Darlington's and Janaki's Chromosome Atlas. The haploid number for *Leucopogon strongylocarpus* was also given in error as $n = 4$.

TABLE 1 (*Continued*)

Genus and Species	Acc. No.	State	Localities	Chromosome Numbers n	Chromosome Numbers $2n$	Pollen Type	Remarks and References
Tribe Epacrideae (*Continued*)							
Andersonia							
A. grandiflora Stschegl.	WA52/	W.A.	Stirling Ra.	—	—	*T*	
A. sprengelioides	WA50/51	W.A.	Albany	13	—	*T*	
	WA52/6		Mt. Dale				
A. coerulea R.Br.	WA50/109	W.A.	Albany	13	—	*T*	Figure 54
	WA52/70		Porongorups				
Richea							
R. sprengelioides R.Br.		Tas.	National Park	13	—	*T*	
R. gunnii Hook.		Tas.		13	—	*T*	
R. gunnii Hook.		N.S.W.	Kosciusko	13	26	*T*	
R. scoparia Hook.		Tas.	National Park	13	—	*T*	
R. dracophylla R.Br.		Tas.	National Park	13	—	*T*	
R. pandanifolia Hook.		Tas.	National Park	13	—	*T*	Figure 57
Dracophyllum							
D. secundum R.Br.		N.S.W.	Lane Cove, Rylstone	13	—	*T*	Smith-White 1948*a*
Sphenotoma							
S. squarrosum R.Br.	WA52/	W.A.	Toolgenup	—	—	*T*	
S. drummondii Benth.	WA52/79	W.A.	Toolgenup	7	—	*T*	Figure 58
S. dracophylloides Sond.	WA52/78	W.A.	Stirling Ra.	6	—	*T*	Figures 59, 60

A polyploid series within the genus is represented by *A. microdonta* ($2n = 16$, Figs. 8 and 9), *A. humufusum* ($2n = 24$), and *A. stomarrhena* ($2n = 32$, Fig. 11). An unidentified species, WA52/13, possibly belonging to the genus, but found in young flower bud only, has a gametic number 6 (Figs. 12 and 13).

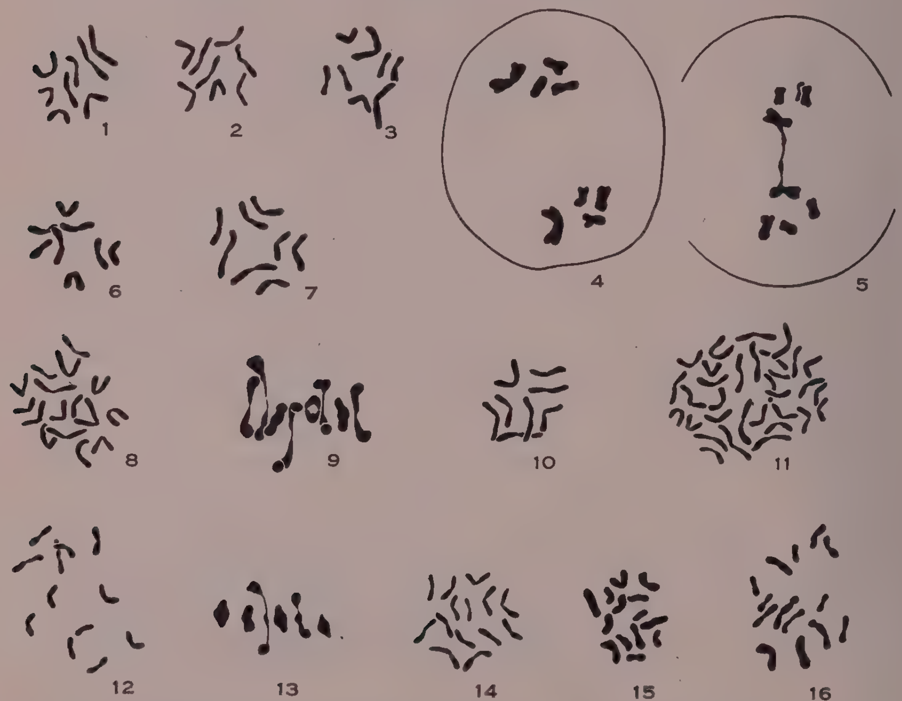


Fig. 1.—*Styphelia laeta*, somatic metaphase in leaf tissue. Fig. 2.—*S. tenuiflora*, somatic metaphase in leaf tissue. Figs. 3-5.—*Astroloma xerophyllum*. Fig. 3.—Somatic metaphase in leaf tissue. Fig. 4.—*M*2. Fig. 5.—*M*2 with residual bridge, no fragment. Fig. 6.—*A. prostratum*, somatic metaphase in leaf tissue. Fig. 7.—*A. tectum*, somatic metaphase in leaf tissue. Figs. 8, 9.—*A. microdonta*. Fig. 8.—Somatic metaphase in leaf tissue. Fig. 9.—*M*1. Fig. 10.—*A. epacridis*, somatic metaphase in leaf tissue. Fig. 11.—*A. stomarrhena*, somatic metaphase in leaf tissue. Figs. 12, 13.—*Astroloma* sp. Fig. 12.—Somatic metaphase. Fig. 13.—*M*1. Fig. 14.—*A. conostephioides*, somatic metaphase in leaf tissue. Figs. 15, 16.—*A. pinifolius*, somatic metaphase in leaf tissue. All × 2600.

Two species, *A. conostephioides* and *A. pinifolius*, are aneuploid ($n = 7$, Figs. 14, 15, and 16). In *A. pinifolius* the karyotype is markedly differentiated (Fig. 16) with differences in chromosome length, and with two pairs of small trabants. In this species meiosis is regular, apart from only occasional bridges, laggards, and other irregularities, which are not noticeably more frequent than in diploid species. A large chromosome pair, observable both in somatic mitoses and in P.M.C. meiosis at *M*1 (cf. Smith-White 1948*a*), cannot be accepted as evidence of numerical diminution following polyploidy and interchange, since it is also present in diploid species.

Significantly, both aneuploid species show a departure from the monad pattern of pollen development characteristic of the diploid and polyploid species. In both, the monad pollen has been replaced by *A*-type segregating tetrads.

Conostephium ($x = 4, 8$).—Pollen *S*-type. Both species examined are tetraploid if $x = 4$ is accepted as the base number for the genus.

Melichrus ($x = 4, 8$).—Pollen *S*-type. The two species of the genus are tetraploid ($n = 8$, Smith-White 1948*a*).

Pentachondra ($x = 7$).—Pollen *T*-type. Only one species has been available. *P. pumila* ($2n = 28$) is probably tetraploid on base number 7. Meiosis is regular.

Trochocarpa ($x = ?$).—Pollen *T*-type. A haploid number 10 was reported for *T. laurina* (Smith-White 1948*a*).

Cyathodes ($x = ?$).—Pollen *S*-type, *T*-type. A genus not represented on the Australian mainland. Counts have been made only at somatic metaphase in leaf buds.

In *C. glauca* and *C. divaricata* the somatic number is 24 (Fig. 17). In *C. parviflora* $2n = 20$, and in *C. adscendens* $2n = 18$ (Fig. 18). In all four species one chromosome pair is of relatively large size.

In both *C. parviflora* and *C. divaricata* some plants are pollen-sterile, young anthers being without sporogenous tissue. Pollen-fertile plants of *C. parviflora* produce *S*-type pollen, but other species have full tetrads.

Brachyloma ($x = 7, 9$).—Pollen *T*-type, *A*-type. Two species have the haploid number 9, regular meiosis, and *T*-type pollen. One of these, *B. scortechinii*, has unique pollen tetrads in which the usual tetrahedral arrangement has been modified to an irregular and sometimes almost linear one. The third species examined, *B. preissii*, has a haploid number 7 (Figs. 19 and 20) with a large bivalent and regular chromosome association. A minute fragment chromosome is present in some nuclei, in addition to the normal complement. In Figure 21 this fragment is shown in the equator of the *A*1 spindle. Bridges (Fig. 22) and laggards are not frequent. *B. preissii* is also exceptional in its genus in the production of *A*-type pollen tetrads.

Lissanthe ($x = 7$).—Pollen *T*-type. In two species the haploid complement is 7 (Smith-White 1948*a*). *L. montana* is tetraploid ($2n = 28$, Fig. 23) or sometimes hexaploid on this base number. The three plants which were found to possess a somatic number of 42 were probably autotriploids within the species since meiosis in each was irregular (Fig. 25). All three species produce tetrad pollen, but *L. montana* possesses a complex gynodioecic polymorphism, with a high frequency of male sterility.

Leucopogon ($x = 4, 6, 11$).—Pollen *S*-type, *S′*-type, *T*-type. A large genus, subdivided into three sections and a number of series (Bentham 1869) on a basis of inflorescence and anther characters.

In § *Perojoa*, the gametic number 6, or polyploidy on this base number, is found in four of the seven recognized series (Fig. 28). Other species in the series have a gametic number 11 (Figs. 26, 27, 29, and 30). There is no conformity between chromosome numbers and the taxonomic series. Associated with this aneuploid number is the *S′*-type modification of the monad pattern of pollen development.

In *L. virgatus* (series 7) two different numbers ($n = 6, 10$) have been determined from collections from widely separated localities and the difference in number is associated with a difference in pollen type. In *L. corifolius* (series 2) two different determinations ($n = 6, 11$) were obtained from the same collection of material. In neither case has a check been possible. In *L. oldfieldii* and *L. cucullatus* (series 7) polyploidy on the secondary number 11 occurs (Figs. 38, 40, and 41).

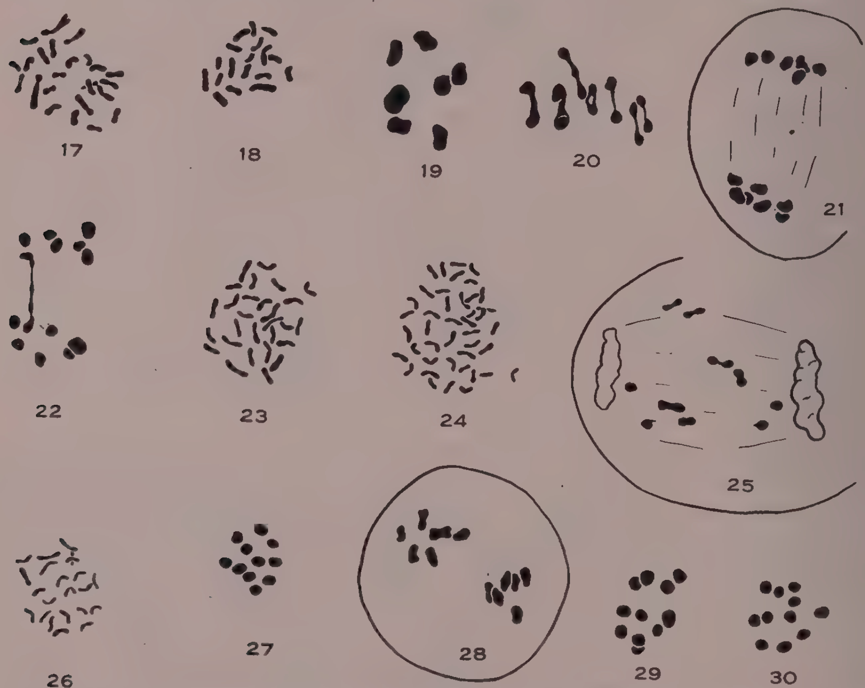
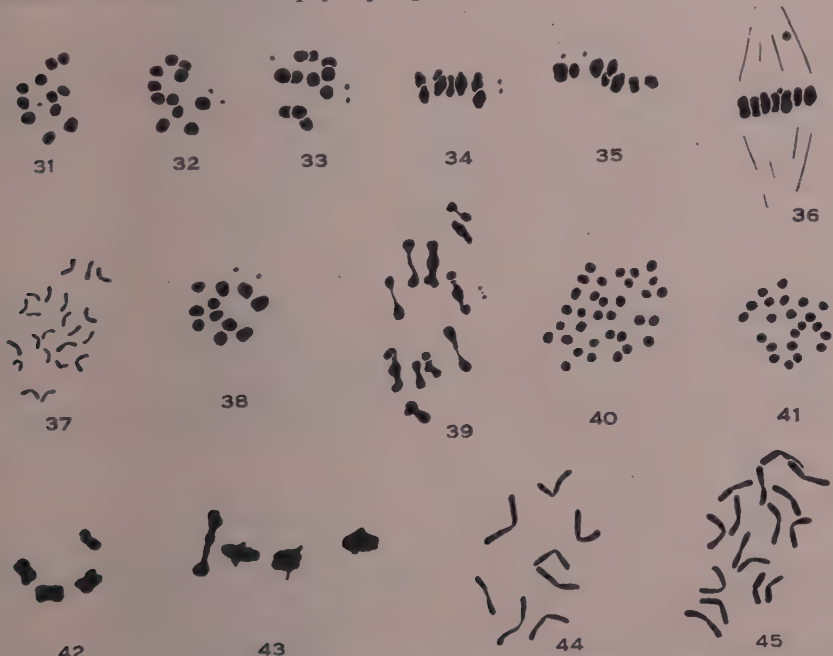


Fig. 17.—*Cyathodes glauca*, somatic metaphase in leaf tissue. Fig. 18.—*C. adscendens*, somatic metaphase in leaf tissue. Figs. 19-22.—*Brachyloma preissii*. Figs. 19-20.—*M*1. Fig. 21.—Late *A*1, with one *B*-chromosome in the spindle. Fig. 22.—*A*1. Bridge, no fragment. Figs. 23-25.—*Lissanthe montana*. Fig. 23.—Somatic metaphase in leaf tissue, $2n = 28$. Fig. 24.—Somatic metaphase in leaf tissue in triploid plant, $3n = 42$. Fig. 25.—*A*1, in triploid, showing univalents and misdivision. Figs. 26-28.—*Leucopogon verticellatus*. Fig. 26.—Somatic metaphase in leaf tissue. Fig. 27.—*M*1. Fig. 28.—*M*2. Fig. 29.—*L. australis*, *M*1. Fig. 30.—*L. capitellatus*, *M*1. All × 2600.

L. revolutus has a karyotype consisting of 11 ordinary bivalents and in addition one or several dot-chromosomes (Figs. 31-36). Dot-chromosomes are not present in all plants, and their number is apparently variable in different pollen mother cells of an anther (Table 2). This variation may be more apparent than real; they may occur, at *M*1, either as univalents or as bivalents, and the latter cannot be distinguished from the former in polar view of the metaphase plate. Also, they may be obscured by the larger chromosomes. If there is an actual variation in their number between different cells of the same plant, they must show anomalous behaviour in

mitosis. Their absence from some plants indicates that they are not essential to survival, and they are interpreted as *B*-chromosomes. Where two such *B*-chromosomes can be identified in side views of *M*1, they may show a paired arrangement on opposite sides of the spindle equator (Fig. 34) or an unpaired arrangement, both being on the same side of the plate (Fig. 36). Minute *B*-chromosomes have been observed occasionally in diploid *L. oldfieldii* (Figs. 38 and 39) and, rarely, in *Brachyloma preissii* (Fig. 21). Wylie (1954) has reported the presence of similar minute chromosomes in two horticultural clones of *Rosa*. There is a remarkable cytological parallelism between the two genera, particularly in the pattern of E.M.C. meiosis in the canina roses and in *Leucopogon juniperinus*.



Figs. 31-36.—*L. revolutus*, illustrating the occurrence of minute *B*-chromosomes at *M*1. Fig. 37.—*L. corifolius*, somatic metaphase in leaf tissue. Figs. 38-40.—*L. oldfieldii*. Fig. 38.—*M*1, $n = 11$ plus *B*-chromosomes. Fig. 39.—*M*1, showing paired *B*-chromosomes. Fig. 40.—*M*1, $n = 33$. Fig. 41.—*L. cuculatus*, *M*1, $n = 22$. Figs. 42, 43.—*L. propinquus*, *M*1, $n = 22$. Fig. 44.—*L. fraseri*, somatic metaphase in leaf tissue. Fig. 45.—*L. biflorus*, somatic metaphase in leaf tissue, $2n = 16$. All × 2600.

The section *Heteranthesis* of *Leucopogon* is a small one; only one species has been examined. *L. hookeri* has a haploid number of 14 chromosomes, and *T*-type pollen. It is often considered to be identical with *Lissanthe montana*. In fact, the two species agree in having similar chromosome numbers, similar tetrad pollen, and similar gynodioecic polymorphism. They have similar distributions in subalpine south-eastern Australia, and are often found together in the Kosciusko region. However, in the field, they can be distinguished by several characters (Table 3) and it is probable that they constitute reproductively isolated populations.

The section *Pleuranthus* includes five series, four of which are represented in the present survey. In two eastern species of series 2, *L. ericoides* and *L. muticus* (Fig. 46), and in four species of series 5 (Figs. 47 and 48), the haploid number is 6.

TABLE 2

FREQUENCY OF POLLEN MOTHER CELLS CONTAINING 0–4 MINUTE B-CHROMOSOMES IN LEUCOPOGON REVOLUTUS

Plant	P.M.C.'s with *B*-Chromosomes				
	0	1	2	3	4
Plant 52/56.3	16	30	11	2	0
Plant 52/56.4	5	20	14	4	0
Total	21	50	25	6	0

Twelve species, in series 1, 3, and 4, have the haploid number 4 (Figs. 42-44), and karyotypes resembling those of *Styphelia*. Tetraploidy occurs in *L. biflorus* (Fig. 45), which belongs to series 4, and the same series includes the permanent triploid *L. juniperinus*. All species of the section have typical *S*-type monad pollen.

TABLE 3

DISTINCTIONS BETWEEN LEUCOPOGON HOOKERI AND LISSANTHE MONTANA

Character	*Leucopogon hookeri*	*Lissanthe montana*
Corolla lobes	Woolly	Glabrous
Leaves	Rather flat	Markedly recurved
Flowering season	December	January-February
Fruit development (Jan.-Feb.)	No fruit from previous season. Fruit ripens before winter	Ripe fruit from previous season. Fruit of previous season ripens in summer

Acrotriche ($x = 9$).—Pollen *T*-type, *A*-type. The four species examined have identical chromosome numbers (Figs. 49-51) and three of these have tetrad pollen. *A. fasciculiflora* produces *A*-type pollen very similar to that found in *Brachyloma preissii*. This species shows a very distinctive karyotype (Fig. 51). Such highly specialised karyotypes are unusual in the Styphelieae, but are also found in *Brachyloma preissii* and *Astroloma pinifolius*.

Monotoca ($x = 12$).—Pollen *S*-type. The two species of the genus have a haploid number 12. No inference is possible about the origin of this set, either as a tetraploid derivative of the 6-chromosome base number, or as a hexaploid of the 4-chromosome series. *M. scoparia* at Bobbin Head and at Newnes, N.S.W., shows sex-polymorphism.

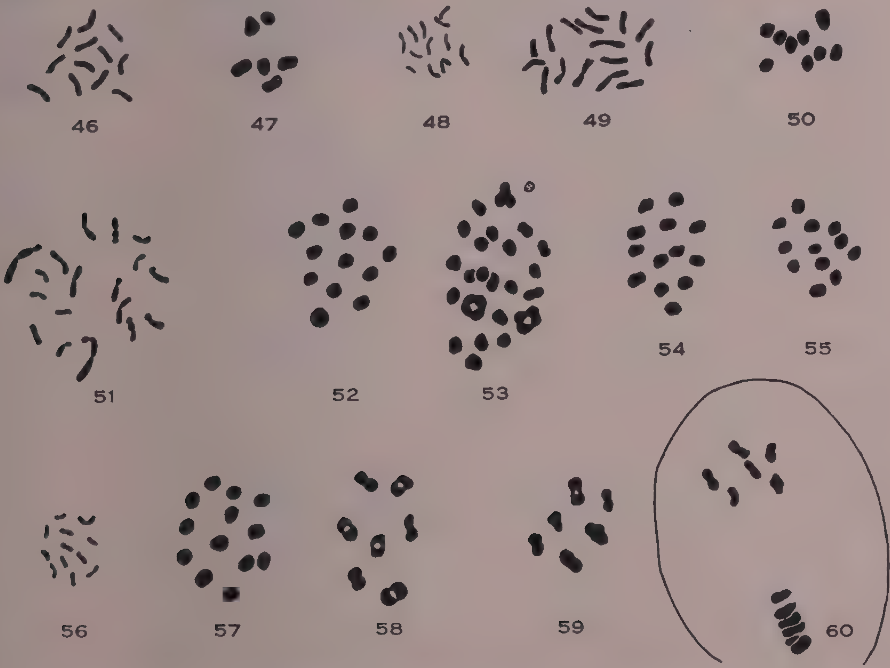


Fig. 46.—*Leucopogon muticus*, somatic metaphase in leaf tissue. Fig. 47. *L. crassifolius*, *M*1. Fig. 48.—*L. strongylocarpus*, somatic metaphase in leaf tissue. Figs. 49-50.—*Acrotriche ovalifolia*. Fig. 49.—Somatic metaphase in leaf tissue. Fig. 50.—*M*1. Fig. 51.—*Acrotriche fasciculiflora*, somatic metaphase in leaf tissue, showing a markedly differentiated karyotype, $2n = 18$. Fig. 52.—*Epacris crassifolia*, *M*1. Fig. 53.—*E. serpillifolia*, *M*1, showing two tetravalents, one trivalent, and one univalent. Fig. 54.—*Andersonia coerulea*, *M*1. Fig. 55.—*Sprengelia ponceletia*, *M*1. Fig. 56.—*Lysinema ciliatum*, *M*2, one plate only, $n = 12$. Fig. 57.—*Richea pandanifolia*, *M*1. Fig. 58.—*Sphenotoma drummondii*, *M*1, $n = 7$. Figs. 59, 60.—*S. dracophylloides*, $n = 6$. Fig. 59.—*M*1. Fig. 60.—*M*2. All × 2600.

Tribe Epacrideae ($x = 6, 7, 12, 13$)

In comparison with the Styphelieae this tribe is less variable in chromosome number, and it is strictly uniform in pollen type. In six genera, the haploid number is 13 (Figs. 52, 54, and 57) with only one case of polyploidy among 24 species (*Epacris serpillifolia*, Fig. 53). In *Sprengelia* and *Lysinema* the haploid number is 12 (Figs. 55 and 56). The major nonconformity in chromosome constitution is found in the western genus *Sphenotoma*, in which haploid numbers of 6 and 7 occur (Figs. 59 and 60).

IV. Discussion

(a) *Evolutionary Development*

The extended list of chromosome numbers necessitates a substantial modification of views expressed by the author (Smith-White 1948*a*) on the primitive basic number and phylogenetic relationships in the Epacridaceae.

In the tribe Styphelieae haploid numbers of 12, 11, 10, 9, 8, 7, 6, and 4 occur, and it might be inferred that these numbers represent a decreasing series involving structural change and centromere loss. That this is not the correct inference is indicated by several considerations.

(i) The karyotypes of *Styphelia* spp. and *Leucopogon* spp. with $n = 4$ are symmetrical, whereas those of *Astroloma pinifolius* ($n = 7$), *Brachyloma preissii* ($n = 7$), and *Acrotriche fasciculiflora* ($n = 9$) are highly asymmetrical. Stebbins (1950) has suggested that asymmetrical karyotypes are likely to be derived.

Table 4

POLLEN TYPES AND CHROMOSOME NUMBERS IN THE STYPHELIEAE

Pollen Type	Total Species	Genera	Chromosome Numbers (haploid)
S	57	*Styphelia, Conostephium, Astroloma, Melichrus, Leucopogon, Monotoca, Cyathodes*	4, 8, 16 6, 12, 24
S′	12	*Leucopogon*	11, 22, 33
T	11	*Pentachondra, Trochocarpa, Brachyloma, Lissanthe, Leucopogon, Acrotriche, Cyathodes*	7, 14 9, 10
A	4	*Astroloma, Brachyloma, Acrotriche*	7, 9

(ii) Polyploid series on base 4 occur in *Astroloma* ($n = 4$, 8, 12, 16) and in *Leucopogon* § *Pleuranthus*. Haploid 8 in *Conostephium* and *Melichrus* also suggests a polyploid derivation. A polyploid series on base 6 is found in *Leucopogon* § *Perojoa* ($n = 6$, 12, 24), and the karyotype of *Monotoca* ($n = 12$) is probably derived from this base number.

(iii) Haploid numbers of 7 and 9 are probably derivatives from a polyploid condition (viz. 4, 8, 7, and 4, 8, 9). This inference is almost obligatory in *Astroloma*, where the usual haploid number is 4. Haploid 7 in *Lissanthe* could be a derivative of the 6-series.

(iv) The association of typical *S*-type monad pollen with the haploid numbers 4 and 6, and with polyploids of the 4 and 6 series, is of paramount significance. Tetrad (*T*-type), segregating (*A*-type), and modified monad (*S′*-type) pollens are found in genera and species which do not belong to the 4-8-12-16 or the 6-12-24 polyploid series (Table 4). The assumption of a reducing series from 12 to 4 demands

an independent and repetitive loss and gain of the peculiar *S*-pattern of development in several phyletic lineages within the tribe.

For these reasons it may be concluded that the basic number in the Styphelieae is either $x = 4$ or $x = 6$. Chromosomal changes have included both polyploidy and aneuploidy. Reduction in number following structural changes and centromere loss is indicated as the origin of the 11-chromosome karyotype in *Leucopogon* § *Perojoa*, and the minute *B*-chromosomes in *L. revolutus* and some other species may possibly represent "naked" centromeres produced as a result of unequal interchange.

Haploid numbers of 13 and 12 are usual in the Epacrideae, in which the pollen is consistently of full tetrad type. The polyploid origin of these karyotypes is indicated by the occurrence of haploid numbers of 6 and 7 in *Sphenotoma*. *Sphenotoma* and the related genus *Dracophyllum* possess extreme morphological specialization, and are vicarious in their distribution, the former in Western Australia and the latter in eastern Australia, Tasmania, New Zealand, and New Caledonia. It could scarcely be maintained that *Sphenotoma* is primitive to *Dracophyllum*, and it certainly is not primitive to the whole tribe. Two alternative hypotheses are possible. Either the base numbers 12 and 13 have originated by amphidiploidy on a number of independent occasions, or the two species of *Sphenotoma* represent reductions, or even reversals, of polyploidy.

The second hypothesis is highly improbable. In the absence of intermediate numbers chromosome diminution following interchanges cannot be entertained. Huskins (1952) has suggested an evolutionary role for somatic reduction but no cases of the reversal of polyploidy have been established.

The first hypothesis is more probable. On the basis of this hypothesis, the cytological constitution of *Sphenotoma* represents a primitive condition, and the basic number for the tribe is $x = 6$. It then becomes likely that $x = 6$ is also primitive for the Styphelieae, and the phyletic relationship required by the morphological characters of the two tribes is supported. The hypothesis demands multiple origins of haploid numbers of 12 and 13, and consequently denies any relationship at the amphidiploid level between the Epacrideae and the Ericoideae.

The Epacridaceae must be granted considerable antiquity. Reid and Chandler (1933) have identified *Leucopogon* in the London Eocene flora, and even if their identification is in error with respect to the genus, the Styphelieae must have had a much wider range in the early Tertiary than they have at the present time. The discovery of *S*-type pollen in early Tertiary beds would be of great value in establishing this inference.

The general picture of the distribution of the Epacridaceae within Australia, with vicarious species and genera in eastern and Western Australia and few species common to both regions (cf. Smith-White 1948*a*, Table 1), is very similar to the distributional pattern of the Boronieae (Smith-White 1954*b*).

Early and late phases in the evolutionary development of the family can be recognized. If the time scale proposed by Crocker and Wood (1947) is accepted, modern species are post-Miocene in origin, but many of the genera must date back

to the Eocene. The phyletic separation of the Epacrideae and Styphelieae, the occurrence of fundamental changes in chromosome structure giving rise to the past chromosomal instability of the Styphelieae, and the origin of the *S*-pattern of pollen development, must be of still greater antiquity.

(*b*) *Taxonomy*

Mueller (1868) and Drude (in Engler and Prantl 1891) reduced many of the genera of the Styphelieae which were established or recognized by R. Brown and by Bentham (1869) to sectional rank within *Styphelia*. Drude's classification was accepted by Maiden (1916), but has not received general recognition in Australia.

A very close relationship between the genera of the Styphelieae is indicated by the similarities in patterns of pollen development, but differences in chromosome number favour retention of the usual generic subdivisions. The large genus *Leucopogon* is a composite one, and includes several sections of equivalent status to other genera. *Leucopogon* § *Pleuranthus* is more nearly related to *Styphelia* than to the other sections of *Leucopogon* itself.

The highest degree of polyploidy is developed in *Leucopogon* § *Perojoa*, and in this section polyploidy ($n = 12$, 24) and secondary polyploidy ($n = 11$) are associated with the retention of primitive inflorescence characters. In § *Pleuranthus*, the inflorescence is greatly reduced, and this reduction is stabilized in genera such as *Melichrus*, *Astroloma*, *Conostephium*, and *Styphelia*.

V. Acknowledgments

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THE USE OF POINT QUADRATS FOR THE ANALYSIS OF HEATHLAND

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Summary

A brief theoretical examination of the relationships between the orientation of leaves on a plant and the area of their projections is made and it is then shown how, for heathland species, inclined point quadrats give appreciably different and usually higher estimates of percentage cover than do vertical point quadrats. The use of inclined point quadrats for estimation of percentage contribution to the vegetation is examined and found to have no real advantage since no increase in precision is obtained with their use. Errors caused by the thickness of point quadrat pins are found to be large for the estimation of percentage cover in the microphyllous heathland vegetation. These can be minimized by the use of a cross-wire sighting tube, but an experiment shows that caution must be exercised in using this device because of the intertangling of the foliage of the various species. Estimates of percentage contribution were hardly affected by pin size.

When pins were randomised independently over the test area, considerably lower variance for both percentage cover and contribution estimates were obtained compared with pins held in frames of 10.

I. Introduction

The various methods of sampling by point quadrats have recently received thorough and critical examination by Goodall (1952). His data were obtained mainly on herbs and grasses from plots in alpine grassland, dune grasses, or wasteland. During 1948 and 1949 point quadrat data had been obtained on heathland at Frankston, near Melbourne, where some aspects of the method were under trial. Subsequently it was thought advisable to examine appropriate sets of data by the statistical treatments developed by Goodall, so as to confirm or reject for the shrubby heathland vegetation the conclusions obtained from analyses of grassland.

Two of his most important conclusions, which have been re-examined, were: (1) that the smaller the diameter of the point quadrat pin the more accurate were the estimates of percentage cover obtained; (2) that point quadrats placed individually, as opposed to the conventional frame holding 10 pins in line, gave greater precision for a given number of quadrats.

The use of pins inclined at an angle of 45° to the ground was introduced by Tinney, Aamodt, and Ahlgren in 1937. They suggested that it would be a more accurate method than using vertical pins because a larger sample of leaf contacts would be taken. Another reason put forward was that the inclined pins were easier to observe in the vegetation; this could apply to short pasture vegetation but is certainly not true in heathland. Since then this method has been used in the United States by a number of people (Henson and Hein 1941; Arny and Schmid 1942; Hein and Henson 1942; Arny 1944; Drew 1944; Rhoad and Carr

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1945; Sprague and Myers 1945; Musser 1948; Leasure 1949). There has been little done to make a critical evaluation of this method. The main testing ground has been the comparison of point quadrat analyses with dry weight analyses and various claims have been made that inclined pins give a closer approximation than vertical ones to dry weight values (Arny and Schmid 1942; Arny 1944; Drew 1944; Sprague and Myers 1945; Leasure 1949). Even so, the results obtained by the two methods do not correspond and correction factors cannot be used since the differences vary with the growth stage of the plants and with the environmental conditions. The two methods measure in different units and the results of point quadrat analyses should be used for their own intrinsic value. Therefore the evaluation of inclined pins should be made by comparison with vertical pins to see if, in fact, the former do give greater precision.

Drew (1944) calculated the standard errors of estimates of percentage of sward obtained with 20 frames of vertical and 20 frames of inclined pins. The analyses were repeated on the same plots after the vegetation had grown 2 in. taller. The standard error was less for inclined pins on the shorter vegetation but greater on the taller vegetation. Tests applied by the author to Drew's data show that the differences between the variances are not significant,* so that his findings are not regarded as conclusive. In the present paper the question will be examined in greater detail and with the aid of improved estimates of variance and the appropriate significance tests.

II. Methods

The point quadrat analyses contained in this paper were obtained on a small plot of heathland measuring 150 ft (14.7 m) by 50 ft (15.2 m). The plot was selected for uniformity in an area of dry-type heathland, on a sandy podzol, once common near the eastern shore of Port Phillip Bay and near Westernport (Plate 1). Trees, which occur sparsely on these heathlands, were excluded.

The vegetation of the plot, fairly typical of the area as a whole, consists of:

(i) A dense layer of microphyllous shrubs averaging 75 cm high and reaching 1 m. Two species, *Leptospermum myrsinoides* Schlecht. and *Leucopogon virgatus* R.Br., dominate this layer. More than 10 shrubby species may be present in an area the size of the plot;

(ii) Below this, a layer dominated by the two perennial herbs *Hypolaena fastigiata* R.Br. and *Lepidosperma concavum* R.Br. In this layer small shrubs such as *Hibbertia acicularis* F. Muell. may occur;

(iii) Geophytic species, such as orchids and *Drosera* spp., forming a sparse ground layer in spring.

A total of 26 species were recorded on the plot. In each of the various lots of 1000 point quadrats, 15-24 species were encountered. Approximately 60 species have been recorded for the whole of this particular area of heathland.

* Bartlett's test was applied to the two pairs of variances and in neither case was the 5 per cent. significance level realized. See Section III(*b*).

The majority of the species are small-leafed and finely branched and therefore very careful observation is required to determine whether or not a given plant part is contacted by point quadrat pins. In addition, there are few gaps in the plant cover revealing bare ground and the depth of the vegetation gives rise to much overlapping of the plant parts. Furthermore, the species are intimately mixed, with branches intertangled, and the delimiting of layers is often a matter of conjecture. A point quadrat commonly contacts several leaves of a number of species. Thus this type of vegetation may be considered a good testing ground for both the observer and the point quadrat method.

The quadrats were located in the plot by stratified randomisation, the plot being divided into five equal strips in each of which an equal number of quadrats were placed at random.

The apparatus used consisted of pins, made from steel wire 4.08 mm in diameter, placed in a frame holding 10 pins at intervals of 8.9 cm. The frame was fitted with a metal stake at each end and was placed in position by pushing the pointed tips of the stakes into the ground. The pins were allowed to fall to the ground under their own weight through metal guide tubes. The pins drop rapidly and the numbers of contacts with vegetation recorded are those made with the side of each pin after its descent. For individual placement of pins, a single stake with a single guide tube was used. Another frame supported the pins at an angle of 45° (hereafter called inclined pins). Other variants of the method are given in later sections of the paper.

The results were calculated according to Levy's (1933) formulae (A) and (D), denoted in this paper as *percentage cover* and *percentage contribution to the vegetation* respectively.

III. Inclined Point Quadrats

(*a*) *Percentage Cover*

The percentage cover of a species is an estimate of the area of ground covered by the projections of the aerial parts of the plants. Since most plants possess parts orientated obliquely this area will vary with the angle of projection.

The nature of this variation can be illustrated by an experiment with a cardboard leaf which was illuminated by a beam of parallel light. The projection of the leaf onto a horizontal surface was recorded on photographic printing paper and the area was measured with a planimeter. The beam of light was placed both vertically and at 45° to the horizontal surface.

When the leaf is lying horizontally, the areas of vertical and 45° projections are the same (Fig. 1A, B. There are small parallax errors due to the nature of the light source used). If the leaf is now rotated in a horizontal plane, the areas of the projections do not alter. The artificial leaf was placed next so that its long axis was at an angle of 45° to, and the short axis parallel to, the horizontal plane. The leaf may be rotated as before, so that its long axis now describes a cone. During this there is no alteration of the area of the vertical projection (Fig. 1C, E, G), but that of the oblique projection will vary considerably, as follows. When the leaf surface is parallel to the beam of light, the projection area is at a minimum (Fig.

1*D*); when normal to the light beam the maximum area is obtained (Fig. 1*F*); when crosswise in the light beam intermediate values are obtained (Fig. 1*H*). Thus the area of the 45° projection may be equal to, less than, or greater than that of a vertical projection. The leaf may be orientated in other ways; for example, if it is suspended vertically then the oblique projection would always have the larger area.

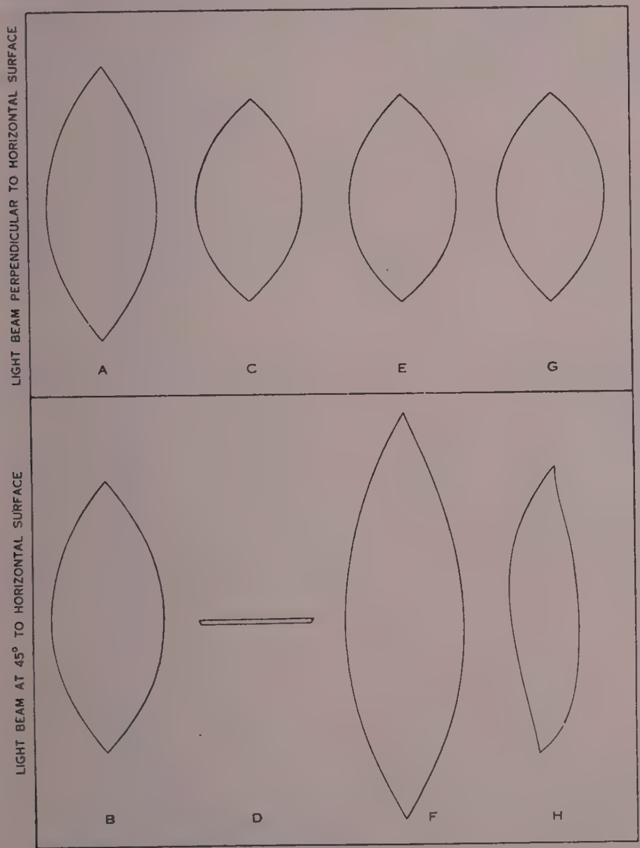


Fig. 1.—Outlines of shadows cast by a cardboard leaf in a beam of parallel light, with the leaf horizontal to (*A*, *B*) or oblique to (*C*-*H*) a horizontal surface and rotated.

From general observations of heathland species, it was expected that inclined projections would cover a greater area of ground. For example, *Lepidosperma concavum* has aerial shoots composed of flat, equitant leaves giving the plant a fan-like appearance (Plate 2, Fig. 1). The leaves rise nearly vertically and are much longer than broad. The upper parts of leaves may curve over under their own weight but the curvature is in different directions for the leaves of a given shoot (Plate 2) and the degree of bending is often lessened by surrounding plants. Measurements of the projections onto a horizontal surface were made by the photographic method. Shoots were rotated so that three positions, two face on and

one edge on to the light beam, were taken at 45°, and only the latter had an area less than that of the vertical projection. It is concluded that inclined pins, which represent the projections at 45° of points on the ground, would give higher frequency of contact with *Lepidosperma concavum*.

TABLE 1

PERCENTAGE COVER ESTIMATED BY VERTICAL AND INCLINED FRAMES OF PINS

Species	Percentage Cover		Significance of Difference (P)
	100 Vertical Frames	100 Inclined Frames	
Leptospermum myrsinoides	47.1	62.6	0.02–0.05
Hypolaena fastigiata	30.4	39.8	0.1–0.2
Leucopogon virgatus	19.1	25.6	0.2–0.3
Lepidosperma concavum	9.4	19.3	0.05
Dillwynia ericifolia	5.1	6.6	0.5–0.7
Monotoca scoparia R.Br.	3.3	6.1	0.3
Epacris impressa	0.9	2.6	—
Trachymene heterophylla F. Muell.	0.0	2.0	—
Banksia marginata Cav.	1.9	2.0	—
Ricinocarpus pinifolius Desf.	0.3	1.5	—
Other species*	3.4	3.4	—
Total	120.9	171.5	
Bare ground (no contact)	5.8	3.1	

* Fifteen other species were recorded, each contributing less than 1 per cent. cover.

For most other species the comparison of the two angles of projection involves not only leaf orientation but also the arrangement and spacing of the individual parts of the foliage of a plant. The projections of these parts frequently overlap and the degree of overlapping, which will vary with the angle of projection, will partly determine the differences in the area of ground covered. Plants with tall canopies having many leaves placed vertically one above another will have a relatively small vertical projection with much overlapping compared with an inclined projection. For the heathland shrubs, whose foliage is usually as deep as broad, inclined pins were expected to give slightly higher estimates of cover than vertical ones.

A trial was conducted on heathland, on horizontal ground, in which percentage cover was estimated by 100 frames each of vertical and inclined pins, independently randomised. The results are presented in Table 1. Species with a percentage cover less than 1 have been grouped together. For the remaining 10 species, inclined pins gave the higher percentage cover. The differences for *Leptospermum*

myrsinoides and *Lepidosperma concavum* are statistically significant as judged by the χ^2-test.

An inclined pin can rotate about a given point on the ground and estimates of cover will depend on the direction of the pin, as already indicated by the cardboard leaf experiment where the rotation of the leaf relative to the light beam was discussed. It is possible that there is an ecological basis for wishing to define the inclined percentage cover in a specific direction, in which case all pins should be placed pointing the same way. Such cases may arise when considering sunlight and rain penetration. In the above experiment, where there was no such basis, any possible bias due to orientation of leaves in a uniform direction was avoided by placing the quadrats pointing to different points of the compass in strict succession of rotation. Each time the frame was moved to a new random position in the plot it was rotated 30° in a clockwise direction, an angle which can be conveniently judged from the face of a pocket watch or compass. In this way, subjective placing of the quadrat is eliminated also.

(b) *Percentage Contribution to the Vegetation*

A pin falling through vegetation will contact, in most cases, more than one part of the same plant, i.e. the parts overlap. As pointed out for percentage cover, the extent of overlapping will differ between vertical and inclined projections according to the orientation of, and pattern of spacing of, the members of the foliage of a plant. Thus the number of contacts per pin will be different when the pin is vertical and inclined and the differences will be strongly affected by the habit of the plant. The suggestion by Tinney, Aamodt, and Ahlgren (1937) that the use of inclined pins would result in a greater number of contacts requires qualification. It is possible for the plant to be so shaped that fewer contacts are made,* as seems likely for some species whose stems are vertical.

No data have been given previously comparing the numbers of contacts per quadrat. In view of this, observations were made on heathland and it was found that, considering only those pins at which a species occurred, the inclined pins had the greater mean number of contacts per pin for the six species examined. These results are shown in Table 2. The significance of differences between means was based on a *t*-test: the variances between frames were calculated on square root transformation of the basic data (see Goodall 1952, p. 30). For *Leptospermum myrsinoides*, *Hypolaena fastigiata*, and *Lepidosperma concavum* the differences are highly significant.

In addition, the case of *Epacris impressa* Labill. is of particular interest. The stems of the shrubs are vertical, bearing a close spiral of small ericoid leaves. A vertical pin striking a shoot will tend to contact a number of leaves in the same orthostichy, whereas an inclined pin will traverse the small width of foliage, making fewer contacts. It was found that the mean number of contacts per pin was 4.83 for vertical as opposed to 3.58 for inclined pins.

There is no reason to assume, as apparently Tinney, Aamodt, and Ahlgren (1937) did, that the variability of number of contacts per pin is less for inclined

* In this discussion pins without contacts are not considered.

pins by virtue of a greater mean value; indeed, a wider range of values may be expected for inclined pins, though the possibility of a smaller variance remains. The variability of these values will be reflected in estimates of percentage contribution, which is the ratio of contacts with a given species to the total number of

Table 2

MEAN NUMBER OF CONTACTS PER PIN ON VERTICAL AND INCLINED PINS

Species	Vertical Pins	No. of Frames	Inclined Pins	No. of Frames	Significance of Difference (P)
Leptospermum myrsinoides	3.41	97	4.40	100	0.001
Hypolaena fastigiata	2.06	92	2.37	99	0.001
Leucopogon virgatus	2.57	77	2.87	93	0.05–0.1
Lepidosperma concavum	1.18	55	1.48	85	0.001
Dillwynia floribunda	2.80	29	3.24	37	0.2–0.3
Monotoca scoparia	3.21	16	3.93	28	0.5–0.6

contacts with all species. When the weighted variances (see Goodall 1952, p. 35) for an equal number of vertical and inclined pins were calculated from the data of the field trial at Frankston, it was found (Table 3) that the variances for inclined pins were the greater for five of the six species considered; for *Lepidosperma concavum*

Table 3

COMPARISON OF THE VARIANCES OF PERCENTAGE CONTRIBUTION OBTAINED FROM 1000 EACH OF VERTICAL AND INCLINED PINS

Species	Weighted Variance	
	Vertical Pins	Inclined Pins
Leptospermum myrsinoides	1.59	1.73
Hypolaena fastigiata	0.52	0.70
Leucopogon virgatus	0.70	0.64
Lepidosperma concavum	0.06	0.10
Dillwynia floribunda	0.22	0.24
Monotoca scoparia	0.36	0.49

the difference is significant ($P = 0.01\text{-}0.02$) as determined by Bartlett's test (Bartlett 1937). The loss of precision may be partly due to larger sampling errors which could arise from the greater opportunity for mis-determination of contacts with inclined pins, added to which greater movement of foliage was necessary to observe the lower part of an inclined pin.

Theoretically, inclined quadrats should give values of percentage contribution different from those obtained with vertical quadrats because the orientation of leaves differs from species to species. In practice it was found that the differences between the methods were slight, as can be seen from Table 4, and may be ascribed to chance variations, as shown by the *t*-test of significance.

TABLE 4

COMPARISON OF PERCENTAGE CONTRIBUTION DETERMINED BY 100 VERTICAL AND 100 INCLINED FRAMES

Species	Percentage Contribution		Significance of Difference (P)
	Vertical	Inclined	
Leptospermum myrsinoides	47.8	48.8	0.6–0.7
Hypolaena fastigiata	18.5	16.8	0.8–0.9
Leucopogon virgatus	15.0	13.8	0.7–0.8
Lepidosperma concavum	3.5	4.9	0.5–0.6
Dillwynia floribunda	3.9	3.8	<0.9
Monotoca scoparia	3.8	4.5	0.8–0.9

IV. SIZE OF QUADRAT

(*a*) *Percentage Cover*

Some pins falling through vegetation will make contact with leaves where, in fact, there is a space between them, and hence point quadrats of finite diameter will over-estimate percentage cover. The error will increase with increase of pin diameter up to the point where it exceeds the maximum size of gaps in the foliage. In heathland, the majority of species are microphyllous shrubs which have relatively small spaces in their canopies and large over-estimations of cover are expected. An attempt to gauge these errors was made by comparing pins of two diameters. One hundred frames of each pin size were recorded on the heathland plot and the percentage cover values are presented in Table 5. The values for significance of differences given are based on a *t*-test; the variance between frames was calculated after angular transformation.

These results revealed three facts. Firstly, the two herbaceous species, *Hypolaena fastigiata* and *Lepidosperma concavum*, were over-estimated by the thicker pins. Secondly, for *Dillwynia floribunda* Sm., a microphyllous shrub, thick pins gave a significantly lower estimate. The reason for this is not clear; though it is possible that the heavier thick pins dislodged the foliage of this species during their downward fall, to the extent of removing it from the final resting position of the pin. The final and most important point is that the differences between pin sizes for the remaining three microphyllous species were insignificant. It would appear that even the fine pins exceed the dimensions of foliage gaps of these species, thereby over-estimating percentage cover by as much as the thick pins. It was

concluded that a very small pin diameter would be required to obtain more accurate (lower) values for the microphyllous species.

Table 5
PERCENTAGE COVER ESTIMATED BY PINS OF TWO DIAMETERS

Species	Pin Diameter (mm)		Significance of Difference (P)
	4.08	1.83	
Leptospermum myrsinoides	47.1	48.9	0.4–0.5
Hypolaena fastigiata	30.4	24.8	0.02–0.05
Leucopogon virgatus	19.1	20.1	0.7–0.8
Dillwynia floribunda	5.1	8.7	0.001
Lepidosperma concavum	9.4	6.4	0.02–0.05
Monotoca scoparia	3.3	5.5	0.1–0.2

In practice, pins finer than 1.83 mm are unsatisfactory since they have too much "lash" of the free end during the fall of the pin; they bend and sway when in position, and they are easily damaged in field use.

Table 6
PERCENTAGE COVER ESTIMATED BY POINT QUADRATS OF TWO DIAMETERS

Species	Quadrat Diameter (mm)		Significance of Difference (P)
	0	1.83	
Leptospermum myrsinoides	50.0	66.5	<0.02
Hypolaena fastigiata	16.5	44.0	<0.001
Leucopogon virgatus	13.5	24.0	0.05–0.1
Lepidosperma concavum	9.0	15.5	0.1–0.2
Dillwynia floribunda	5.0	5.5	0.8–0.9
Epacris impressa	10.0	12.5	0.7–0.8
Aotus villosa Sm.	3.0	7.0	0.3–0.5
Cassytha glabella R.Br.	2.0	8.5	0.05–0.1
Hibbertia fasciculata R.Br.	0.5	3.5	0.3–0.5
Pteridium aquilinum (L.) Kuhn	7.0	5.5	0.8–0.9
Others	1.0	1.0	—
Total	117.5	193.5	
Bare ground (no contact)	8.3	3.0	—

Reduction of quadrat size can be achieved with the cross-wire apparatus devised by Goodall (1952). This gives a good approximation to a true point and

should lead to the most accurate estimates of percentage cover. A comparison of values obtained by this means and by pins of 1.83 mm diameter is given in Table 6, the data for which were obtained from a 1 sq. m. plot of heathland, taking 200 quadrats of each type at random. The effect is clear. The cross-wire quadrats gave the lower values for all but one of 10 species. For a number of species there are striking differences, which are significant for *Leptospermum myrsinoides* and *Hypolaena fastigiata*, as shown by χ^2-tests. There is little doubt that pins of 1.83 mm diameter cause marked over-estimation of both microphyllous shrubs and the herbaceous species.

TABLE 7

PERCENTAGE COVER DETERMINED BY THE CROSS-WIRE APPARATUS BEFORE AND AFTER CLIPPING

Species	Percentage Cover		Significance of Difference (P)
	Before Clipping	After Clipping	
Leptospermum myrsinoides	57	49	0.2–0.3
Leucopogon virgatus	18	17	0.8–0.9
Dillwynia ericifolia	6	4	<0.5
Hypolaena fastigiata	10	23	0.01–0.02
Hibbertia acicularis	12	9	>0.5
Other short species	5	7	0.5–0.7

The use of the cross-wire apparatus presents some difficulty in that it is necessary to sight through a mass of vegetation, up to a metre in depth, which is a mixture of tall and short species whose foliage is often intertangled. Consequently it is sometimes difficult to determine whether or not a species of the lower layers is present in a quadrat; and when the uppermost foliage is pulled aside to view plants lower down, the latter move also. Hence the possibility arises that short species may be underestimated.

To see if the cross-wire apparatus introduced any such systematic error, observations were made on a 0.5 sq. m. quadrat in the following way. After a sample of 100 quadrats had been taken, the vegetation was clipped down a distance of 15-20 cm, to a uniform level. In doing so only *Leptospermum myrsinoides*, *Leucopogon virgatus*, and *Dillwynia ericifolia* Sm. were cut, leaving *Hypolaena fastigiata* intact so that its stems were protruding above the general level of the clipped plants. Then another 100 quadrats were recorded. The comparison of the two analyses is set out in Table 7, where the column of significance of differences is based on χ^2-tests.

It was found that cutting the three species did not greatly reduce their percentage cover since much of the plants remained at a lower level. Clipping removed much of the leaf material of these plants and what remained consisted largely of grey and brown stem material. This change of foreground colour made it easier to observe the foliage of short species such as *Hibbertia acicularis* but the estimate of

cover did not alter significantly. The estimate of *Hypolaena fastigiata* was more than doubled after clipping, showing that this species could be underestimated in normal circumstances. The virtually leafless stems of this species were intermingled with, and obscured by, the foliage of the other tall plants, so that pulling aside the vegetation failed to reveal their presence in a quadrat.

(*b*) *Percentage Contribution to the Vegetation*

Estimates of percentage contribution will be affected by pin diameter, though to a less extent than for estimates of cover. The various species will be over- or underestimated, depending on the size of the errors they cause with thick pins relative to their contribution. In practice such effects were found to be slight, as can be seen from Table 8. For *Lepidosperma concavum* only does the difference reach significance, as determined by *t*-tests.

TABLE 8

PERCENTAGE CONTRIBUTION OF HEATHLAND SPECIES TO THE VEGETATION ESTIMATED BY 1000 PINS EACH OF TWO DIAMETERS

Species	Pin Diameter (mm)		Significance of Difference (*P*)
	4.08	1.83	
Leptospermum myrsinoides	47.8	48.8	0.7–0.8
Hypolaena fastigiata	18.5	14.7	0.3–0.4
Leucopogon virgatus	15.0	13.6	0.3–0.4
Dillwynia floribunda	3.9	7.7	0.4–0.5
Lepidosperma concavum	3.5	2.4	0.02–0.05
Monotoca scoparia	3.8	4.9	0.8–0.9

V. DISTRIBUTION OF QUADRATS

The conventional point quadrat method makes use of a frame holding 10 pins in line. Goodall (1952) has shown that the variance within frames is less than that between frames, with the result that a number of pins placed individually will give greater precision than an equal number in frames. An experiment was conducted on heathland, in which 1000 pins grouped in frames and 1000 placed individually were used, with the following results.

(*a*) *Percentage Cover*

The observations on individual pins were grouped at random into lots of 10 and the variance between groups of 10, whether at random or in frames, was calculated after angular transformation. For all species the frames gave the higher variances (Table 9), the differences being significant in three cases (Bartlett's test).

(b) *Percentage Contribution to the Vegetation*

For estimates of percentage contribution the weighted variances between 100 frames are compared with those between 1000 individually placed pins (Table 10).

TABLE 9

VARIANCE OF PERCENTAGE COVER ESTIMATES BETWEEN GROUPS OF 10 PINS

Species	Variance		Significance of Difference (P)
	100 Groups in Frames	100 Random Groups	
Leptospermum myrsinoides	234.32	108.48	<0.001
Hypolaena fastigiata	164.05	104.57	0.02–0.05
Leucopogon virgatus	214.85	133.44	0.01–0.02
Dillwynia floribunda	140.82	111.65	0.3–0.5
Lepidosperma concavum	162.02	141.57	0.3–0.5
Monotoca scoparia	106.92	90.85	0.3–0.5

Placing the pins singly over the plot resulted in strikingly smaller variances. For all species except *Lepidosperma concavum* the differences between variances are significant ($P < 0.001$).

TABLE 10

VARIANCE OF ESTIMATES OF PERCENTAGE CONTRIBUTION FROM FRAMES AND INDIVIDUAL PINS

Species	Variance	
	Between 100 Frames	Between 1000 Pins
Leptospermum myrsinoides	1.588	0.554
Hypolaena fastigiata	0.515	0.258
Leucopogon virgatus	0.701	0.310
Dillwynia floribunda	0.212	0.079
Lepidosperma concavum	0.058	0.054
Monotoca scoparia	0.364	0.010

These results mean that, for both percentage cover and percentage contribution, fewer pins need to be used to attain any given degree of precision if placed singly; for some species only half or one-third of the number in frames would be required.

VI. Discussion

The question of the use of inclined or vertical point quadrats for the estimation of percentage cover cannot be answered in general terms. The area covered by a vertical projection is a simple concept expressing the horizontal spread of plants and this type of information is generally required in descriptive work, in comparison of areas of vegetation, or in following the spreading of vegetation. On the other hand, it is difficult to relate the concept of oblique projection to features of the species since it depends upon complex relationships between the vertical and horizontal components of leaf orientation, of spacing between leaves, and of plant shape. It can be defined only in terms of a specified angle and direction. There will be problems, however, generally associated with climatic factors, for which oblique pins would be appropriate. For example, the measurement of the area illuminated by the sun under a tree canopy at a given time has been made by Mr. D. Ashton (personal communication) using an oblique cross-wire sighting device. The angle and direction of the point projection corresponded to that of sunlight at the specified time.

On sloping ground, pins may be placed either vertically or normal to the surface, both positions having a fixed direction. The orientation of small herbs and prostrate species may be related to the angle of slope but taller species, especially the larger shrubs and trees, usually remain upright and the orientation of their foliage is independent of the slope. In the former plants, the leaves lie parallel or nearly so to the ground and consequently the percentage cover would be the same for both positions of the pin. For the upright species, cover would be estimated differently by the two methods and the same arguments apply as those given above for vertical and oblique pins. Hence, in general, vertical pins are preferred.

Inclined pins have been used previously by a number of investigators to estimate percentage contribution (botanical composition of pastures). There is little to recommend this modification of the method. The inclined pins made more contacts with vegetation, as was expected, but there was no gain in the precision of estimation of percentage contribution. It is suspected that large sampling errors are introduced and this effect may well apply to other tall vegetation. The values of percentage contribution do not differ appreciably between the two methods. The net result in using inclined pins is an increase in the work required to collect the data.

Gross over-estimation of percentage cover occurred when using wire pins and therefore it is advisable to use a cross-wire sighting device when values for cover alone are required. Considerable care must be exercised with this apparatus since an important species may be underestimated if obscured by other plants in dense vegetation. Quadrat size had little effect on estimates of percentage contribution and the more durable thick pins may be preferred for practical reasons.

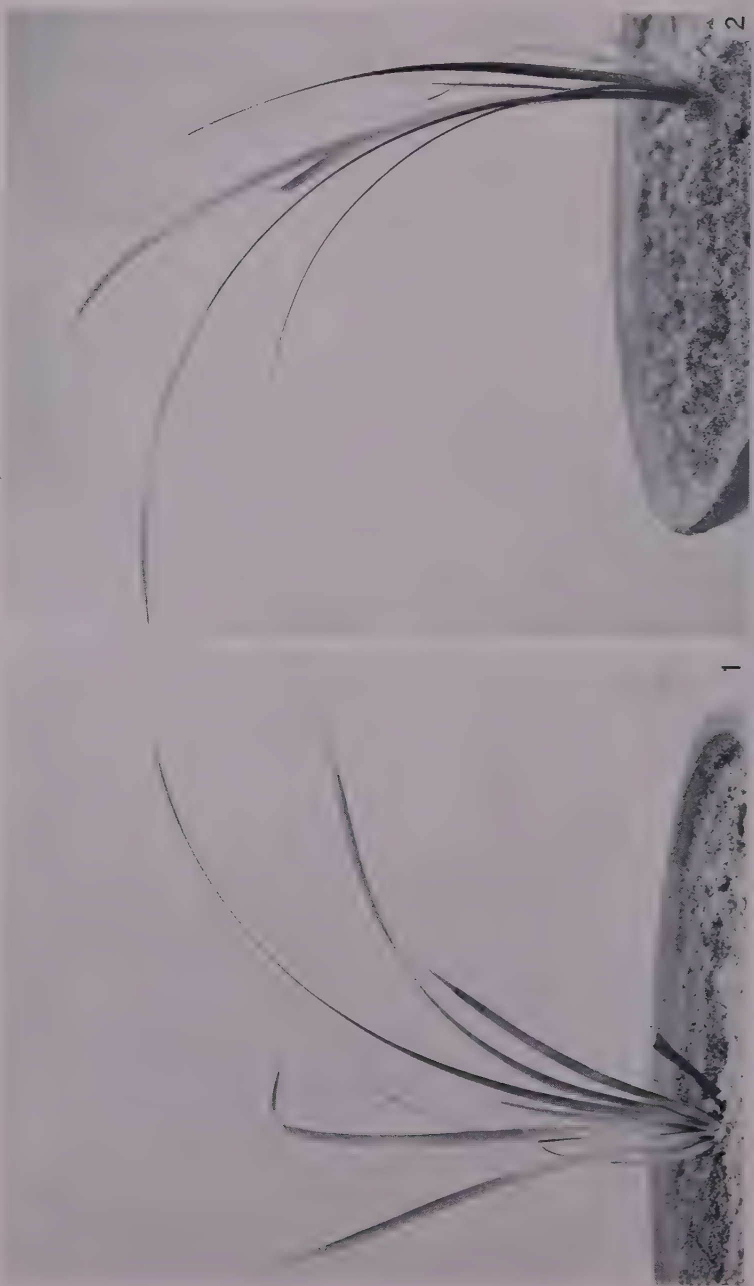
It was clearly demonstrated that individual placing of pins gave much greater precision than pins in frames. This finding substantially confirms the results obtained in grassland communities by Goodall (1952), who fully discussed the implications.

POINT QUADRATS FOR ANALYSIS OF HEATHLAND

1

2

POINT QUADRATS FOR ANALYSIS OF HEATHLAND



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Explanation of Plates 1 and 2

Plate 1

Fig. 1.—General view of heathland at Frankston, showing dense shrub layer 4 ft tall and isolated tree-clump of *Eucalyptus viminalis* Labill.

Fig. 2.—Close up of shrub layer showing its structure in more detail. In the foreground are *Leptospermum myrsinoides*, *Epacris impressa*, *Banksia marginata* Cav., *Dillwynia ericifolia*, and others. (Photos. by D. Ashton.)

Plate 2

Fig. 1.—Face-on view of a shoot of *Lepidosperma concavum* collected at Frankston.

Fig. 2.—The same shoot as in Plate 2, Figure 1, photographed edge on. (Photos. by E. Matthaei.)

FIELD IDENTIFICATION OF DICOTYLEDONS: A PUNCHED CARD SYSTEM FOR THE IDENTIFICATION OF FAMILIES

By N. Hall* and R. D. Johnston*

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Summary

A punched card key for use in the identification of dicotyledons to a family level is described. It has advantages over the ordinary dichotomous key in that it allows early use of the most conspicuous or most selective characters of an unknown plant. It also facilitates the identification of incomplete material.

The key is based on Hutchinson's (1926) descriptions. Cards for his 264 families have been prepared.

A sample card shows the characters used and the method of clipping, and an illustration of the card set shows the distribution of various characters between families.

I. Introduction

Many field workers (for example, foresters, ecologists, and regional surveyors) who lack a specialized training in systematic botany find identification of plant species difficult. This is particularly true of those who work under conditions which make reference to herbarium taxonomists either inconvenient or impossible. The usual printed key is sometimes useless because the available plant material is incomplete. Often, obviously unusual characters of an unknown plant are useless because the normal key does not mention them.

On the other hand a card-sorting system can be used with incomplete material. The order of sorting can be varied so that the most conspicuous or most selective characters can be used at an early stage, and the need for making use of characters about which information is lacking or difficult to obtain is eliminated.

A card-sorting system also has the advantage that the cards for additional families can be added to a set, or cards can be removed when operating in a restricted area, without involving any basic change in the key. Disadvantages of such a system, compared with a dichotomous key, are that it is relatively expensive to produce, and it is comparatively bulky. Because of this last fact the scope of any one sorting system is limited by the number of cards which can be conveniently handled. We have therefore made a key for the identification of plants only to a family level.

II. Previous Work

Punched cards have been used for many years for office and business records throughout the world. The various applications of the system and the principles of sorting have been comprehensively discussed by Casey and Perry (1951).

Dadswell and Eckersley (1941) have used card-sorting systems in the identification of timber. The first application in this field was for species determination,

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but cards were subsequently adapted for use in referring an unknown timber to its correct family. These card-sorting systems have enabled a timber specimen to be placed correctly in its family, and sometimes in its genus, when botanical material was inadequate for identification. Such determinations have been invaluable in dealing with specimens from such comparatively unknown regions as New Guinea.

Botanists have not been as active as wood technologists in adapting card-sorting systems to problems of identification. Dunkley (1939) in Uganda, and Walker (1948) in Malaya, produced systems to aid in local identification of tree species, and de Rosayro (1953) has suggested that a similar key may be produced for Ceylon. Metcalfe (1953) drew attention to the successful use of card-sorting systems in the study and identification of timbers. He suggested that similar use could be made of card systems in the study of the systematic anatomy of higher plants. Hall and Johnston (1953) have briefly reviewed the use of cards in forest botany.

A card-sorting system for families of dicotyledons based on morphological characters was developed by one of the authors (N.H.) in New Guinea during 1944, whilst he was attached to a technical unit. He was concerned with the identification of timbers but, because at that time New Guinea trees were incompletely known and named timber specimens were not available for comparison, identification had to be based on morphological characters.

A card was designed using the characters given by Hutchinson (1926) in his family descriptions and his key based on artificial groups. The resulting card system worked, but in view of the limited botanical literature available in New Guinea during war-time it was not possible to produce a complete coding of the families.

Since that time a card system has been developed for species identification in the genus *Eucalyptus* (Hall and Johnston 1953). The interest shown in this and the demand for it encouraged the authors to redesign the card originally used in New Guinea and to extend the system to include all families of dicotyledons.

III. Design of the Cards

The original card system produced in 1944 was based on the classification of the dicotyledons according to Hutchinson (1926). This basis has been maintained, since Hutchinson is a reasonably well-known and widely used reference book, is written in English, and appears suitable for the non-specialist. In addition, the number of families in this classification—264—represents about an average number based on present-day concepts, and the family limits (although not necessarily the higher groupings) are generally acceptable to contemporary taxonomists.

In considering the size of the card, a compromise had to be made between having information on as many characters as possible set out on the cards and keeping the cards small enough to be conveniently handled. The card adopted measures 11.7 by 8.5 in. and provides 156 sorting holes. Characters have been allotted to 143 of the holes, leaving 13 free for the inclusion of such extra information as may be required by the specialist. (See Figs. 1 and 2.)

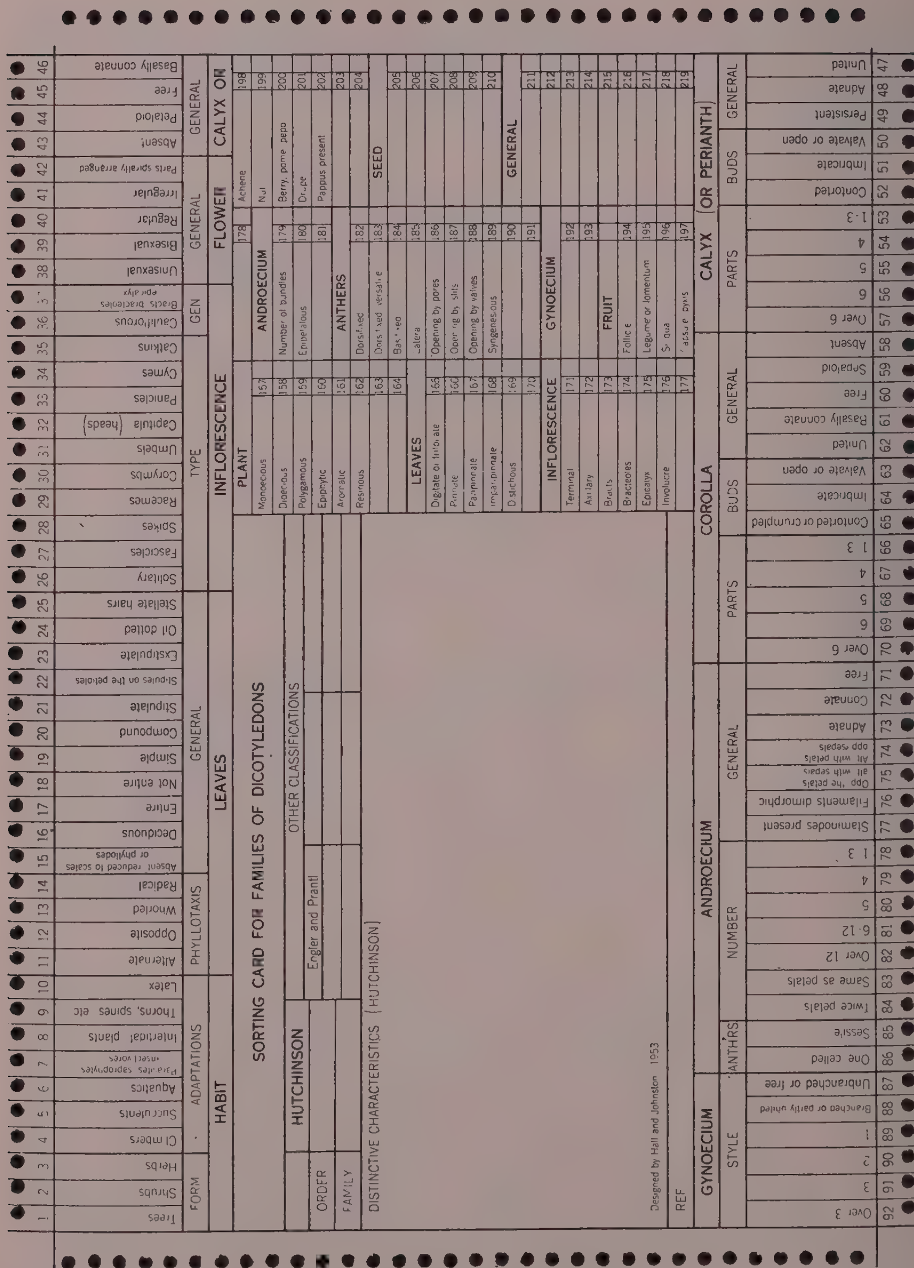

Fig. 1.—A typical card, face view.

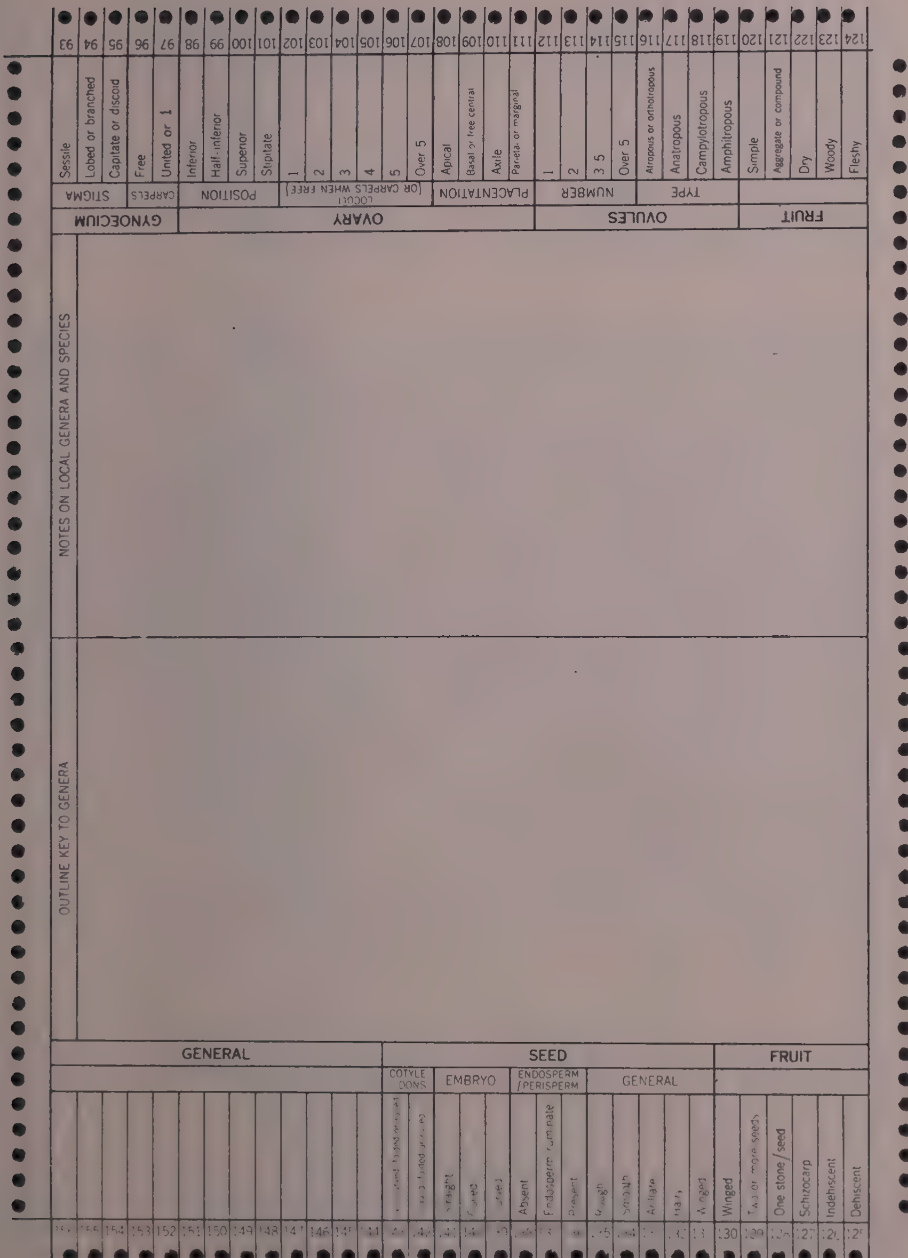

Fig. 2.—A typical card, back view.

In selecting characters for use in sorting, certain general principles were followed. It is important that all aerial parts of the plant should be represented, in order that when only incomplete material is available, it will be possible to use those characters which are present. All characters should be important at the family level and as many as possible should be macroscopic. This does not debar the use of certain microscopic characters, such as the type of ovules, for use in the determination of difficult specimens.

As an indication of the distribution of characters amongst the various plant parts, the following summary shows the respective allocations.

Habit	10	Calyx/perianth	15	Ovary	14
Leaves	15	Corolla	13	Ovules	8
Inflorescence	12	Androecium	16	Fruit	11
Flower summary	5	Gynoecium	11	Seed	13

Terms employed have been based on Hutchinson, but considerable reference has been made to the illustrated glossary given by Lawrence (1951). The simplest terms consistent with clarity of meaning have been used in referring to botanical features. For example, the terms free and united carpels have been used rather than apocarpous and syncarpous ovary, and free and united (petals) rather than polypetalous and gamopetalous corolla. For convenience and to eliminate the need for reference to the above works, a list of definitions of all terms used on the cards has been compiled, and is included in the guide to the use of the card system. It is felt, however, that some comment may be necessary on several of the terms used.

14. *Radical.*—When leaves form a rosette at ground level, whether or not there are also leaves present on the stem.

16. *Deciduous.*—This character is fairly selective; it is apparent when the trees are leafless and other characters thus not available. The alternative state, evergreen, is not selective and it is difficult to be sure at first sight that a tree is evergreen, so the latter character has not been coded.

42. *Parts spirally arranged.*—This number is clipped for families in which the sepals, petals, stamens, or carpels are arranged spirally.

46. *Basally connate.*—The conventional descriptions of sepals or petals are that they are poly- or gamosepalous or -petalous. There is a limited number of families which have sepals and petals either completely free or connate only at the base for a small portion of their length. Were only two categories used, i.e. free and united, it would be necessary to code such families as both free and united, thus grouping more families than desirable in the united group.

88. *Style—branched or partly united;* 94. *Stigma—lobed or branched.*—It was found that different authors sometimes described the same structure as either a branched style or a lobed stigma. Typically the two conditions are distinctive but when the branching is near the apex of the style and the stigmatic surfaces of the branches appear to join, the real condition is not particularly obvious. Where authors have disagreed and illustrations indicate an intermediate condition it has been the practice to code for both characters.

131-143. *Seed*.—Here, more than in any other section, the characters used have been limited by the published information available. Very few descriptions devote more than a few words to the seeds and the authors are not aware of any recent publication which describes the seed characters of all families of flowering plants. Martin (1946) described and illustrated the seeds of a large number of families. Considerable use was made of his work on the comparative internal morphology of seeds to code characters 139-143. Some additional information was secured from the "Woody Plant Seed Manual" of the United States Forest Service (1948). The only other publication which describes seeds of plant families appears to be that of Gaertner (1788-1805).

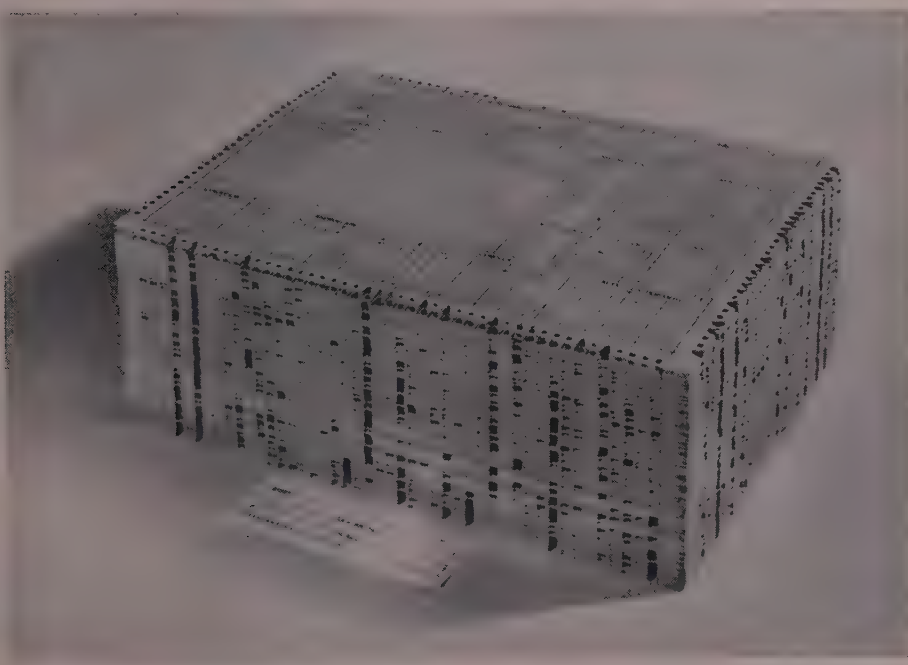

Fig. 3.—The complete punched card key, showing clipping for two edges of the cards.

Characters have been coded according to their appearance, and detailed anatomical study should not be necessary. For instance, in apetalous families which have a petaloid calyx the coding of the calyx/perianth is repeated for the corolla, so that users of the cards will not have to distinguish between the two conditions. If they are able to do so then sorting will be more rapid. A further example is in the number of loculi in the ovary. The ovary may be two-celled but by the development of false septa it may appear four-celled. In such a case the family would be coded for both conditions. Similarly, when parts such as stipules or calyx are present on the developing organ but fall at or before maturity, the card would be clipped to indicate both occurrence and absence of the parts in the family.

The occurrence of any character in a family is shown by clipping the appropriate number on the card for that family. Then all families in which a particular character is represented can be selected by passing a suitable sorting rod (e.g. steel knitting needle) through the appropriate holes in the card set, lifting, and shaking gently, so that cards which are clipped for that number will fall.

Since clipping for any character does not exclude the possibility that the alternative hole might also be clipped, sorting must always be on a positive basis. That is, any further sorting must be carried out on the cards selected, not on those remaining on the rod.

It is important to use the most definite character first, leaving those which are less definite until later. Certain characters have a more selective value than others and these should be used as early as possible in the procedure. An indication of the selective value of the characters is given if one looks across the edges of the stacked cards (Fig. 3) and notes the relative frequency of clipping for various characters, e.g. with leaves, "oil dotted" is selective whilst "alternate" is not.

In addition to those coded on the edges of the card and hence capable of being mechanically sorted, a number of characters have been shown on the card face, and their occurrence in any family can thus be noted. These characters are generally of minor importance either because of very limited or very wide occurrence; but in some cases, characters have had to be placed on the card face because, notwithstanding their importance for sorting, the information available is incomplete.

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BISACCATE SPOROMORPHS FROM AUSTRALIAN PERMIAN COALS

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Summary

The structure and distribution of bisaccate microspores isolated from coals and shales of the Australian Permian are discussed. Microspores assigned here to the sporotypes *Lueckisporites* Potonié & Klaus, *Alisporites* Daugherty, *Florinites* Schopf, Wilson, & Bentall, and *Pityosporites* Seward have been described and a number of new sporomorphs designated. *Vestigisporites* n. spt. is instituted as a new sporotype.

Comparisons are made between Australian Palaeozoic bisaccate forms and similar types from approximately contemporaneous deposits in other parts of the world, and the possible affinities of early two-bladdered microspores discussed.

I. Introduction

Bilaterally symmetrical microspores, equipped with bladder-like extensions of the exoexine and structurally similar to the pollens of certain present-day conifers, first appear in both the northern and southern hemispheres in terrestrial sediments of Upper Carboniferous or Lower Permian age. The most ancient type of microspore with this type of structure is a mono-bladdered form, *Florinites* Schopf, Wilson, & Bentall, which appears first at the base of the Westphalian in Europe and persists at least into the Lower Rotliegendes. *Parasporites maccabei* Schopf, from the Carbondale Group of Illinois (probably Westphalian C), is the oldest known truly bisaccate form, but its large size and functionally trilete germinal scar differentiate it from superficially similar late Palaeozoic types. The sporotype *Illinites* Kosanke, from the Upper McLeansboro beds of Illinois (presumed to be Stephanian), is also clearly bisaccate, but in his designation Kosanke (1950) states that it is functionally trilete. Florin (1938-40, pt. 5, Tables 163-164, Fig. 10) has recorded *Pityosporites* from the Middle Stephanian of Europe, and Imgrund (unpublished data) found bisaccate types in the Permian coals of the Kaiping basin. Potonié and Kremp (1954) state that *Pityosporites* occurs in the lower Rotliegendes and the Zechstein of Europe, and bisaccate grains have been recorded from the Upper Zechstein (Lueck 1913), Keuper (Daugherty 1941), and Lias (Nathorst 1908; Reissinger 1939). Luber (1938, 1939) figured "conifer" type pollens from the Permian coals of the Kuznetsk and Minusinsk basins, and Daugherty (1941) referred certain bisaccate grains from the Upper Trias of Arizona to *Pityosporites* and *Alisporites*.

It is, however, from the coals of Gondwanaland that bisaccate microspores have been isolated in greatest abundance and variety. Owing to the present lack of knowledge of the spores associated with the southern *Rhacopteris* flora, the antiquity of bisaccate forms in Gondwanaland is uncertain; but they occur in large numbers in the Talchir boulder bed of India (Virkki 1945), the Greta coals of New

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South Wales (Dulhunty 1946), the Lower Coal Measures of Tasmania (Dulhunty and Dulhunty 1949), the lowest coal beds at Collie, W.A. (Balme 1952), and the Irwin River coals of Western Australia. It appears, therefore, that the plants producing these microspores were well established in Gondwanaland by the beginning of the Permian period. If the composition of coal seam spore floras is a reliable guide to floral trends these plants increased in abundance during the Permian, for a proliferation of winged types occurs in the Tomago and Newcastle Stages in New South Wales (Dulhunty 1946), the Upper Bowen of Queensland (de Jersey 1946), and the upper coals at Collie (Balme 1952). Virkki's (1945) work also shows that the Daltonganj coals (Lower Barakar) contain a large variety of bisaccate types and Ghosh and Sen (1948) note their abundance in the Raniganj seams. The Triassic coals of Ipswich, Qld, contain very similar winged types to those of the Upper Permian seams of eastern Australia (de Jersey 1949).

II. Affinities of Bisaccate Microspores

Pollen grains possessing inflated air-sacs are produced today only by certain members of two coniferalean families, the Abietineae and Podocarpineae. For this reason earlier authors (e.g. Nathorst 1908; Seward 1914) usually attributed any isolated fossil bisaccate grains to the Coniferales. Pollen grains assignable with fair certainty to conifers are known from the Jurassic of Victoria (Cookson and Pike 1954), but palaeobotanical experience suggests that coniferalean affinities should not necessarily be attributed to isolated bisaccate grains from pre-Jurassic sediments.

Potonié (1952) considers that the bladders on saccate grains arose from the separation of exoexine and intexine and he regards the *Florinites* form as the progenitor of truly biwinged pollens. The radially symmetrical sporomorph *Endosporites* Wilson & Coe, which was related to *Florinites* by Schopf, Wilson, and Bentall (1944), is functionally trilete and, at least in part, of lycopodiaceous origin (Chaloner 1953), so that the presence of inflated air-sacs is in itself no indication of gymnospermous affinity. *Florinites*, however, is known to have been produced by the Upper Palaeozoic coniferalean genera *Lebachia* and *Ernestiodendron* (cf. Florin 1938-40, pt. 3, Tables 105-106, Figs. 20-21; pt. 4, Tables 121-122, Fig. 27) and structurally similar grains were borne by certain members of the Cordaitales. The earliest known bilaterally symmetrical bladdered microspores are therefore gymnospermous in origin.

Other groups of plants are known to have produced bisaccate spores during the Mesozoic. They occur in *Caytonanthus* (Harris 1937, p. 44), the pollen-bearing organ of *Caytonia*, species of which have been described from the Jurassic of Yorkshire (Thomas 1925; Harris 1937, p. 44) and the Rhaetic of east Greenland (Harris 1937, p. 40). Similar microspores were also found by Harris (1935, p. 137) in the Greenland beds, associated with the cups of *Leptostrobus longus* and the scale leaves of *Czekanowskia hartzi*. In the Molteno beds (Upper Trias) of South Africa the pollen-bearing organ *Pteruchus*, which occurs in association with a number of seed-bearing inflorescences of the pteridosperm family Corystospermaceae, is known to have produced small bilaterally symmetrical winged pollen grains (Thomas 1933).

It has been suggested by Virkki (1937, 1945) and other Indian authors (e.g. Sen 1953) that certain species of *Glossopteris* produced bisaccate spores. There is no direct evidence for this although Seward (1933) seems to suggest that H. H. Thomas had related certain biwinged types to *Glossopteris*. Whether *Glossopteris* produced bisaccate microspores or not, it can have been only one member of a group of plants which did so during the Upper Palaeozoic and Lower Mesozoic Eras. The persistence of typically Permian forms in the Ipswich coals with an associated *Thinnfeldia-Taeniopteris* flora and the occurrence of very similar types in the European Trias is sufficient evidence for this.

III. Classification of Sporomorphs

Potonié and Kremp (1954) have grouped all Palaeozoic spores possessing air-sacs under the division Saccites, a name attributed to Erdtman. Saccites has been further subdivided into Polysaccites (Cookson 1947), Disaccites (Cookson 1947), and Monosaccites (Chitaley 1951). Under the subdivision Disaccites Potonié and Kremp have placed all previously described two-bladdered genera of Palaeozoic and early Mesozoic fossil spores, viz. *Vesicaspora* Schemel, *Parasporites* Schopf, *Illinites* Kosanke, *Alisporites* Daugherty, *Lueckisporites* Potonié & Klaus, and *Pityosporites* Seward.

The classification of the wealth of bisaccate forms found in Australian Permian coals into stratigraphically useful sporomorphs presents considerable difficulty. It is not easy to decide the allowable limits of variation for individual sporomorphs in an essentially artificial taxonomic system, and the problem is accentuated by the fact that all specimens have been compressed and distorted into thin lamellae by the compaction of the sediments which enclosed them. The variations to be expected in a single type of microspore are illustrated by the photographs of acetolysed and compressed pollen grains of *Podocarpus alpina* shown in Plate 1, Figures 1-5.

Disregarding possible monstrosities (Plate 4, Fig. 44) the normal variation of several of the types is considerable and classification of specimens near the extremes of variation is always somewhat subjective.

A morphological feature of many pre-Jurassic bisaccate grains which has, until recently, received little attention is the presence on their proximal faces of parallel transverse thickenings of the exine, which often merge into the roots of the bladders. These striate thickenings are present on a wide variety of forms, sometimes prominently displayed, sometimes only faintly discernible. Their precise function is uncertain although they are possibly part of the germinal mechanism. The widespread occurrence of microspores bearing these striae (they have been recorded from Permian and Triassic sediments in India, Australia, China, Europe, and North America) suggests that they have phylogenetic significance. Those with proximal striae have in the past usually been classified under *Pityosporites* (e.g. Virkki 1937, 1945; Daugherty 1941; Ghosh and Sen 1948) but it seems undesirable to suggest that they "agree in size and form with recent Abietineous genera" as Seward's (1914) generic diagnosis demands. The recent creation of the

genus *Lueckisporites* Potonié & Klaus to embrace bisaccate spores bearing proximal striae is therefore welcome.

Dimensions given in the following descriptions are, unless otherwise specified, based on measurements of specimens preserved in full proximo-distal orientation. For specimens with a circular or subcircular equatorial section, body diameter has been taken as the maximum width of the central body, measured in a direction parallel to the line of attachment of the bladders.

IV. Descriptions of Sporomorphs

Lueckisporites Potonié & Klaus

Lueckisporites Potonié and Klaus, 1954, p. 531.

Lueckisporites fusus n. spm.

Plate 1, Figs. 6-10

Probable synonymy

P40B Dulhunty 1945 (in part).
P40B (Dulh.) de Jersey 1946 (in part).
Spore 90, spore 91 Virkki 1945.
P40B (Dulh.) Balme 1952.

Type locality.—Cardiff Seam, Collie, W.A.

Dimensions (25 specimens).—Central body 28-48 μ (mean 38 μ). Total bladder span 81-146 μ (mean 112 μ).

Body circular or subcircular, proximal surface of exine thickened, usually dark in colour with faintly discernible proximal striae 4-5 μ wide. Bladders large compared with body, subcircular in equatorial section, and ornamented with a fine internal reticulum. Germinal area narrow, longitudinal dehiscence slit sometimes visible.

Discussion.—Seldom common in any single maceration but widespread in Gondwanaland deposits. Forms which appear to agree with the above diagnosis have been recorded in the following localities.

NEW SOUTH WALES: Newcastle and Tomago Stage coals.
WESTERN AUSTRALIA: Collie; Irwin River; Wilga.
TASMANIA: Mount Pelion; Cradoc (Dulhunty and Dulhunty 1949).
QUEENSLAND: Mount Mulligan (de Jersey 1946).
INDIA: Pali beds, Rewa (Virkki 1945); Raniganj (Ghosh and Sen 1948).

Lueckisporites cancellatus n. spm.

Plate 2, Figs. 11-15

Type locality.—Seam at 377 ft, South Wallarah No. 5 bore, N.S.W. (Newcastle Stage).

Dimensions (50 specimens).—Body 21-32 μ (mean 27 μ). Total bladder span 40-70 μ (mean 54 μ).

Body circular or subcircular, exine thick, dark in colour, proximal face with striate thickenings, usually about 6 in number. Bladders variable in size and

development, one often larger than the other and distally inclined. Germinal area narrow, sometimes with a longitudinal dehiscence slit.

Discussion.—Structurally similar to *L. fusus* but smaller and bladders more variable in size and form. *L. cancellatus* is particularly abundant in certain coals from the Newcastle Stage of New South Wales. It resembles bisaccate types figured by Virkki (1937, Plate 32, Fig. 3) from above the Talchir Boulder Bed, Kathwai.

Lueckisporites multistriatus n. spm.

Plate 2, Figs. 16-20

Probable synonymy

P40D Dulhunty 1945.

Type locality.—Seam at 679 ft, South Wallarah No. 3 bore, N.S.W. (Newcastle Stage).

Dimensions (10 specimens).—Body 33-45 μ (mean 40 μ). Total span 46-61 μ (mean 55 μ).

Body oval, elongated parallel to the proximal striations. Exine fairly thin, proximal striae narrow, numerous, and regularly spaced. Bladders small, stubby, set on the distal side of the grain, and inclined distally. Germinal area wide but no opening observed. Tends to flatten in semi-lateral view.

Discussion.—*L. multistriatus* is a very characteristic form identified in a number of Newcastle and Tomago Stage coals, and in the Homeville seam (Greta Stage).

Lueckisporites amplus n. spm.

Plate 3, Figs. 24-28

Probable synonymy

P38A Dulhunty 1945.
P40C Dulhunty 1945 (in part).
P38A (Dulh.) de Jersey 1946.
P40C (Dulh.) de Jersey 1946 (in part).
Spores 80, 82, 83 = *Pityosporites* spp. Virkki 1945.
P38A (Dulh.) Balme 1952.

Type locality.—Seam at 688 ft, South Wallarah bore, N.S.W. (Newcastle Stage).

Dimensions (30 specimens).—Body 48-76 μ (mean 59 μ). Total bladder span 84-131 μ (mean 111 μ).

Body circular or oval in proximo-distal view, exine fairly thin, faintly granulate, and marked by broad but often only faintly discernible striae on the proximal face. Germinal area about 20 μ wide with a germinal rupture often visible (Plate 3, Figs. 24-25). Bladders regular in size and disposition, usually a little larger than the central body with a finely reticulate internal ornament.

Discussion.—Common and widespread in Gondwanaland deposits. Forms agreeing with the above diagnosis have been recorded from the following localities.

NEW SOUTH WALES: Greta, Tomago, and Newcastle Stages.
WESTERN AUSTRALIA: Collie; Irwin River (Balme 1952 and unpublished data).
TASMANIA: Upper and Lower Permian coals (Dulhunty and Dulhunty 1949).
QUEENSLAND: Upper Bowen (de Jersey 1946); Ipswich (de Jersey 1949).
INDIA: Pali beds, Rewa; above Talchir Boulder Bed, Kathwai (Virkki 1945).

Lueckisporites limpidus n. spm.

Plate 3, Figs. 29-32; Plate 4, Figs. 33-35

Type locality.—Lithgow Seam, Kandos Colliery, N.S.W.

Dimensions (40 specimens).—Body 30-44 μ (mean 38 μ). Total bladder span 55-85 μ (mean 70 μ).

Morphologically very similar to *L. amplus* but smaller and with a thinner finely granulate body exine. In some specimens the air-sacs surround the body equatorially, so that the spore becomes mono-bladdered. Frequently compressed laterally or semi-laterally.

Discussion.—Very common in many New South Wales seams from the Newcastle and Tomago Stages. Similar but slightly different forms occur in the Collie coals, and Virkki's spores 77 and 85 from the Pali beds, Rewa, probably belong to this category.

Lueckisporites phaleratus n. spm.

Plate 3, Figs. 36-38

Type locality.—Seam at 688 ft, South Wallarah No. 5 bore, N.S.W. (Newcastle Stage).

Dimensions (12 specimens).—Body 30-45 μ (mean 41 μ). Total bladder span 75-90 μ (mean 85 μ).

Body circular or subcircular. Exine thick and dark in colour. Proximal cap faintly granulate with indistinct striate thickenings. Germinal furrow clearly delineated by thickened raised lips about 5 μ wide. Bladders regular in size and development, ornamented with fine external granules and an internal reticulum.

Discussion.—Rare but widely distributed in seams of the Newcastle Stage of New South Wales.

Pityosporites Seward

Pityosporites Seward, 1914, p. 23.

Pityosporites giganteus n. spm.

Plate 2, Figs. 21-23

Type locality.—Greta Seam, Hebburn No. 2 Colliery, N.S.W.

Dimensions (10 specimens).—Body 62-84 μ (mean 74 μ). Total bladder span 110-150 μ (mean 126 μ).

Spore body oval or subcircular in proximo-distal compression; lens-shaped in lateral view. Exine thin, finely granulate, proximal cap little thickened. Bladders small compared with body, inclined distally, ornamented with fine granules or faint reticulations. Dehiscence by distal rupture.

Discussion.—One of the largest bisaccate types identified in Australian coals. Rare in the Greta seam but observed in fairly large numbers by one of the authors (B.E.B.) in a coal from Tarleton, Tas.

Alisporites Daugherty

Alisporites Daugherty, 1941, p. 98.

Alisporites milvinus n. spm.

Plate 4, Figs. 39-40

Type locality.—Lithgow seam, Kandos Colliery, N.S.W.

Dimensions (9 specimens).—Body 42-70 μ (mean 55 μ). Total bladder span 62-85 μ (mean 75 μ).

Body oval in proximo-distal view. Exine fairly thick, dark in colour, and unornamented. Bladders relatively small, crescentic, finely granulate with an internal reticulum. Clearly defined fusiform germinal furrow.

Discussion.—A rare and somewhat variable form from the Newcastle Stage of New South Wales, *A. milvinus* recalls the pollen of *Caytonanthus* and the spore types 74 and 75 of Virkki (1945).

Vestigisporites n. spt.

The name *Vestigisporites* is proposed for bisaccate spores of unknown affinities having the following characteristics:

Spore body circular or oval in proximo-distal orientation, exine thin without marked proximal thickening, smooth or faint granulate. Proximal face bearing a short transverse slit or fold which recalls a monolete tetrad scar. Bladders attached to body equatorially and symmetrically placed on either side of the central body, rather variable in size and shape, sometimes joining to form a single air-sac (see Plate 6, Figs. 54-56, Figs. 62-64). Bladder ornament fine reticulate or granulate. Wide germinal furrow on distal face.

Discussion.—*Vestigisporites* differs from previously described Palaeozoic bisaccate microspores in its transverse "monolete" slit on the proximal face. Virkki's (1945) spore 81 probably belongs to *Vestigisporites*, and *Saccrimalia monstruosa* Luber (Luber 1939) appears from that author's illustration to be structurally similar.

Vestigisporites rudis n. spm.

Plate 6, Figs. 54-57

Type locality.—Greta Seam, Hebburn No. 2 Colliery, N.S.W.

Dimensions (20 specimens).—Body 52-96 μ (mean 78 μ). Total bladder span 112-161 μ (mean 139 μ).

Body circular or subcircular. Exine thin, fine granulate. Short transverse slit on proximal face, passing through proximal pole. Bladders large, symmetrically placed on either side of the grain, sometimes joining to form a single bladder surrounding the central body equatorially. Bladder ornament granulate or fine reticulate.

Discussion.—Common in seams of the Greta Stage, N.S.W., and seen also in coal from the Illamatha Mine, Mersey, Tas.

Vestigisporites spm. "A"

Plate 6, Figs. 58-64

Synonymy

P40G Balme 1952.

Type locality.—Seam at 688 ft, South Wallarah bore, N.S.W. (Newcastle Stage).

Dimensions (25 specimens).—Body 32-60 μ (mean 46 μ). Total bladder span 60-85 μ (mean 77 μ).

Body circular or subcircular. Exine thin, smooth or fine granulate, no marked proximal thickening. Short transverse slit on proximal face. Dehiscence by distal rupture. Bladders small, crescentic, in some specimens encircling the grain equatorially.

Discussion.—*Vestigisporites* spm. "A" is a common and variable form in the Newcastle and Tomago coals of New South Wales and the seams of Collie, W.A. It probably embraces at least two different sporomorphs which cannot yet be satisfactorily separated. *Saccrimalia monstruosa* Luber and *Pityosporites* sp. (spore 81) Virkki (1945) appear to belong to this category.

Florinites Schopf, Wilson, & Bentall

Florinites Schopf, Wilson, and Bentall, 1944, p. 56.

Florinites eremus n. spm.

Plate 5, Figs. 45-48

Synonymy

P38B Balme 1952.

Type locality.—Main seam, Co-operative Colliery, Collie, W.A.

Dimensions (30 specimens).—Total bladder span 100-138 μ (mean 121 μ). Maximum bladder width 76-113 μ (mean 99 μ).

Consists of a small circular central body enveloped on all but the distal face by a large subellipsoidal bladder. Central body almost always absent and appears to separate easily from the bladder. Internal reticulum on bladder strongly developed.

Discussion.—The most common saccate type in the Western Australian Permian coals of Collie, Wilga, and Irwin River. A few similar types have been recognized in Newcastle and Tomago Stage coals in New South Wales, and Virkki's (1945) spore 31 is morphologically comparable but larger.

Florinites ovatus n. spm.

Plate 5, Figs. 49-52

Synonymy

P40F Balme 1952.

Type locality.—Seam at 174 ft, No. 6 bore, North-East Basin, Collie, W.A.

Dimensions (30 specimens).—Total bladder span 46-74 μ (mean 65 μ), bladder width 36-65 μ (mean 50 μ).

Complete spore oval in proximo-distal compression. Consists of a central oval body (short axis 28-48 μ) surrounded by a single bladder with a narrow line of junction on the distal face. Body not clearly defined and appears only as an oval darkened patch in the centre of the spore. Bladder with fine reticulum.

Discussion.—Resembles *F. eremus* but considerably smaller and more regular in form. Common in all Collie coals and observed also in Newcastle Stage seams in New South Wales.

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Explanation of Plates 1-6

All magnifications × 500.

Plate 1

Fig. 1.—*Podocarpus alpina.* Distal view.

Fig. 2.—*P. alpina.* Lateral view showing distal inclination of bladders.

Fig. 3.—*P. alpina.* Unexpanded grain.

Figs. 4-5.—*P. alpina.* Lateral and sublateral views.

Figs. 6-10.—*Lueckisporites fusus* n. spm.

PLATE 2

Fig. 11.—*Lueckisporites cancellatus* n. spm. Proximal view.
Figs. 12-14.—*L. cancellatus* n. spm. Distal view.
Fig. 15.—*L. cancellatus* n. spm. Lateral view.
Figs. 16-20.—*Lueckisporites multistriatus* n. spm.
Fig. 21.—*Pityosporites giganteus* n. spm. Semi-lateral view.
Figs. 22-23.—*P. giganteus* n. spm. Distal view.

PLATE 3

Figs. 24-26.—*Lueckisporites amplus* n. spm. Distal view.
Fig. 27.—*L. amplus* n. spm. Proximal view.
Fig. 28.—*L. amplus* n. spm. Lateral view showing proximal thickenings.
Figs. 29-30.—*Lueckisporites limpidus* n. spm. Proximal view.
Fig. 31.—*L. limpidus* n. spm. Semi-lateral view.
Fig. 32.—*L. limpidus* n. spm. Lateral view. Unexpanded grain.

PLATE 4

Figs. 33-34.—*Lueckisporites limpidus* n. spm. Distal view.
Fig. 35.—*L. limpidus* n. spm. Proximal view. Unexpanded grain.
Figs. 36-38.—*Lueckisporites phaleratus* n. spm. Distal view.
Figs. 39-40.—*Alisporites milvinus* n. spm. Distal view.
Figs. 41-42.—*Lueckisporites* spm.—P40E Balme 1952.
Fig. 43.—*Lueckisporites* spm.
Fig. 44.—*Lueckisporites* spm. Aberrant grain.

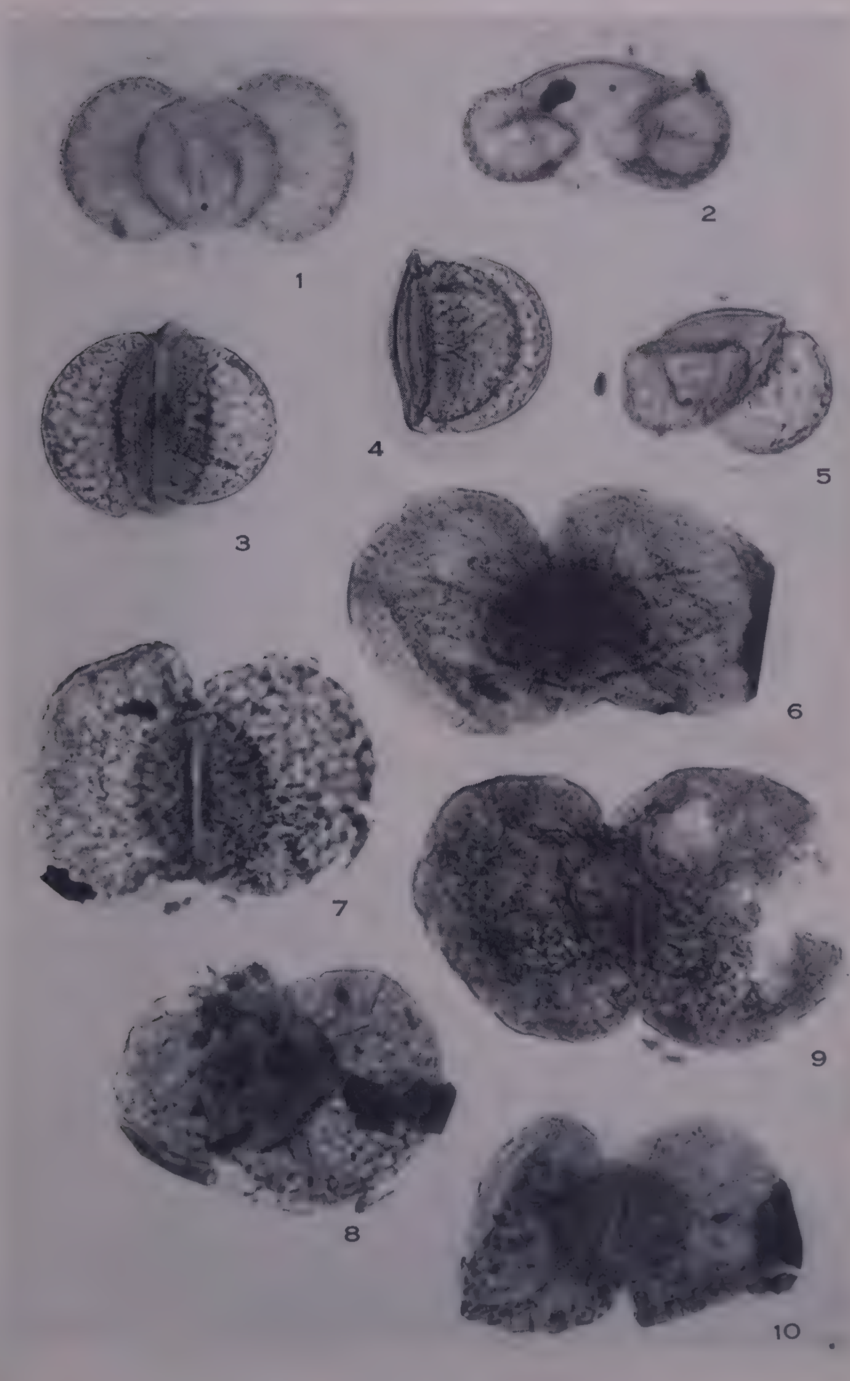
PLATE 5

Fig. 45.—*Florinites eremus* n. spm. Distal view showing body.
Fig. 46.—*F. eremus* n. spm. Proximal view.
Fig. 47.—*F. eremus* n. spm. Body missing.
Fig. 48.—*F. eremus* n. spm. Proximal view showing body.
Figs. 49-52.—*Florinites ovatus* n. spm.
Fig. 53.—Cf. *Endosporites* spm.

PLATE 6

Figs. 54-57.—*Vestigisporites rudis* n. spm.
Figs. 59-64.—*Vestigisporites* spm. "A".

BISACCATE SPOROMORPHS



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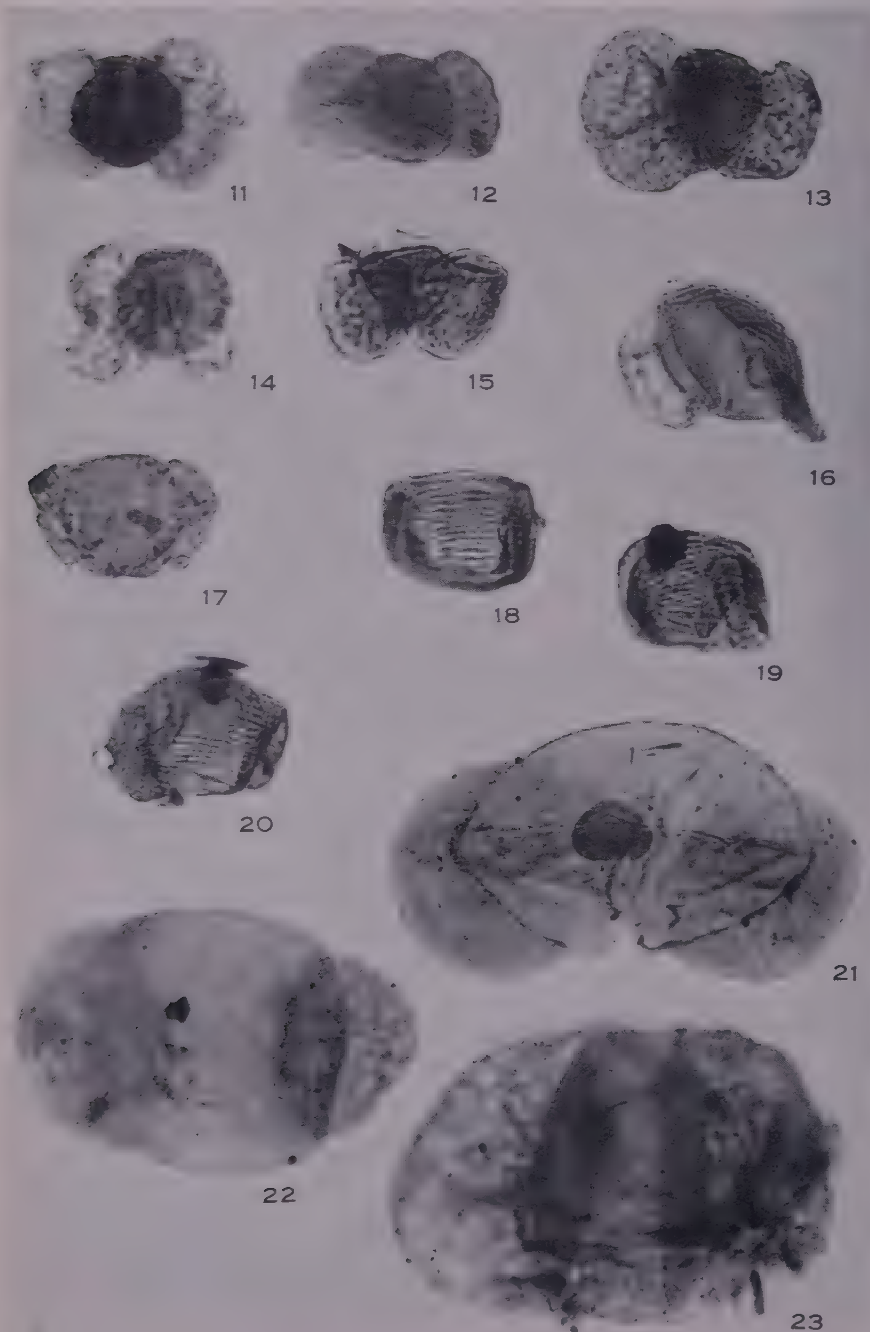

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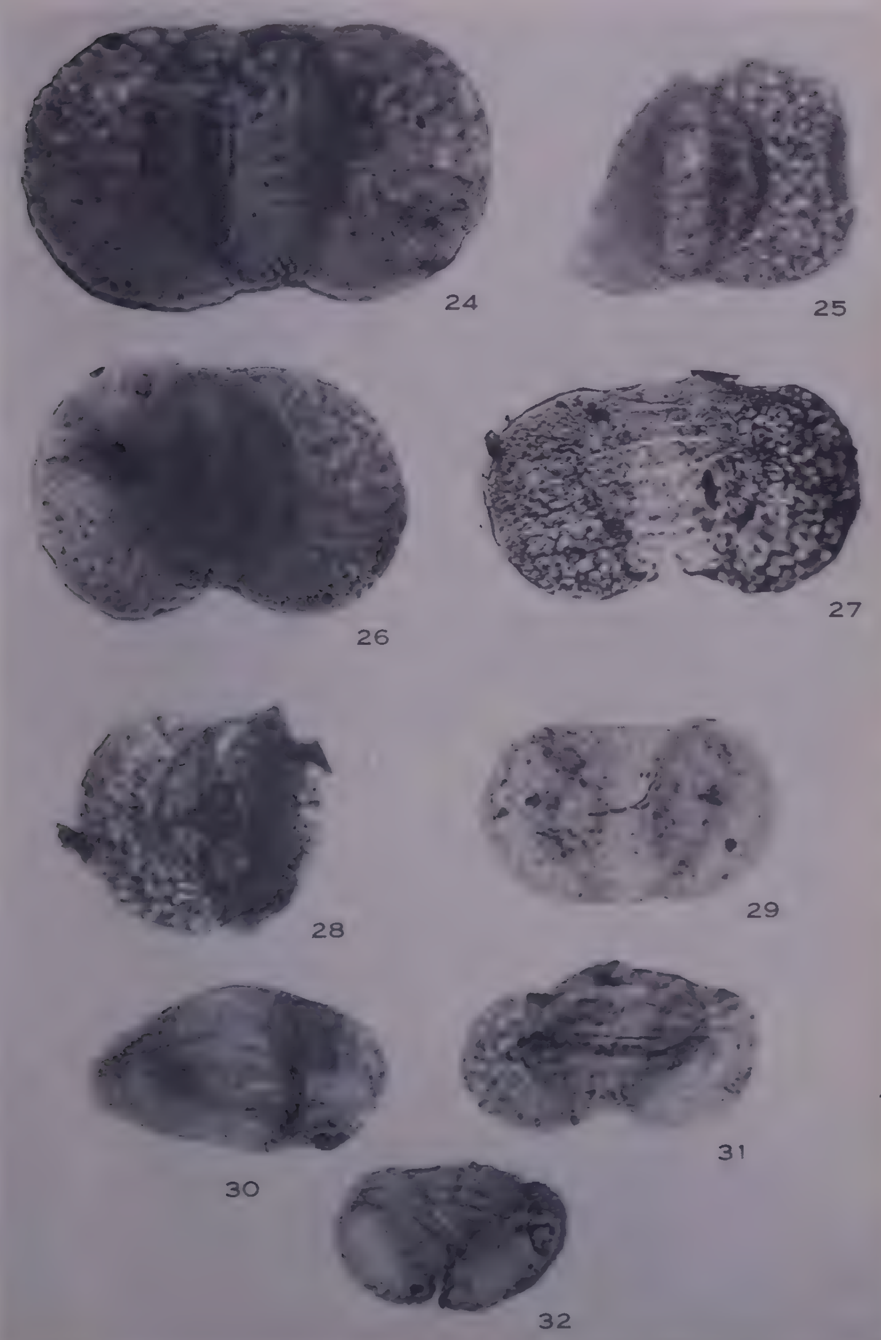

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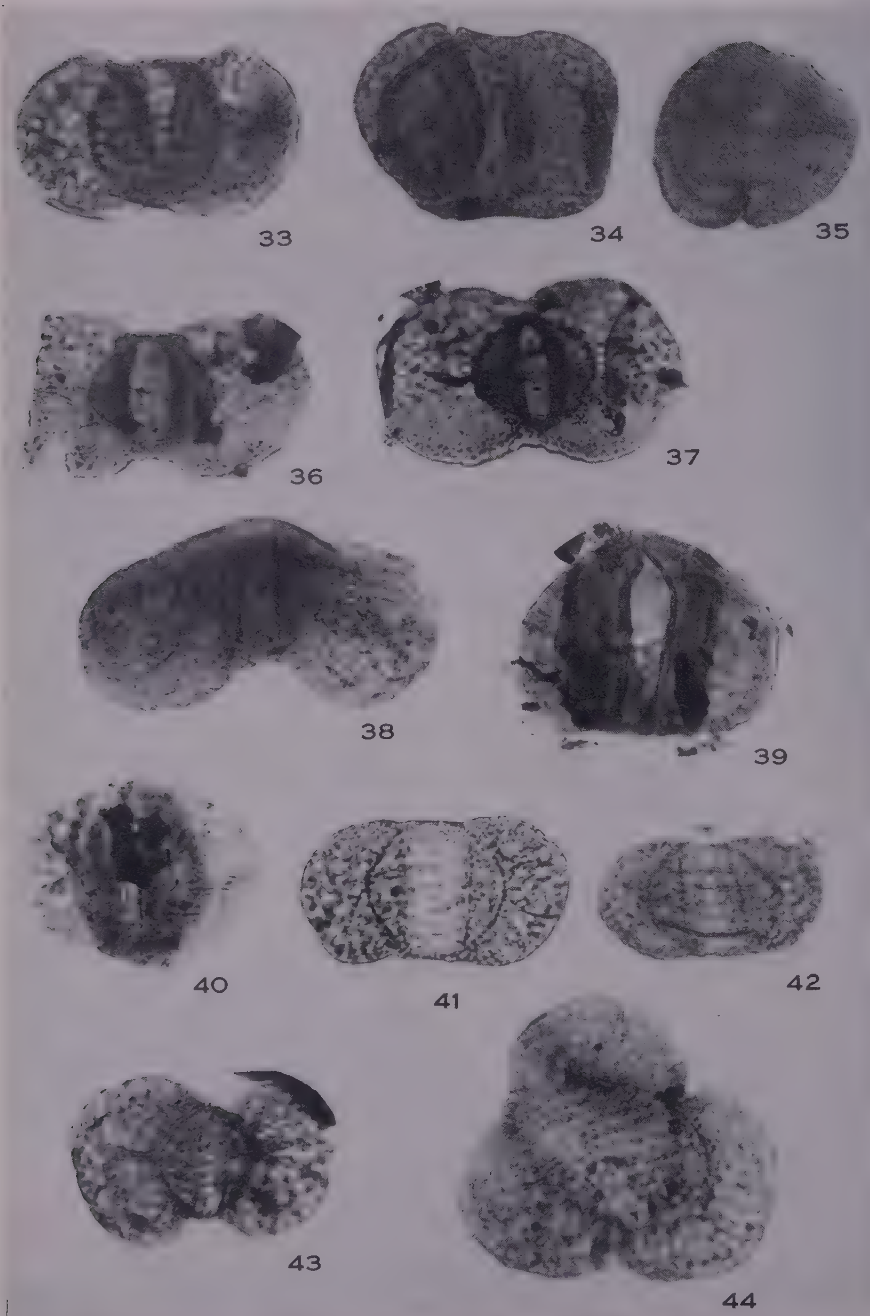

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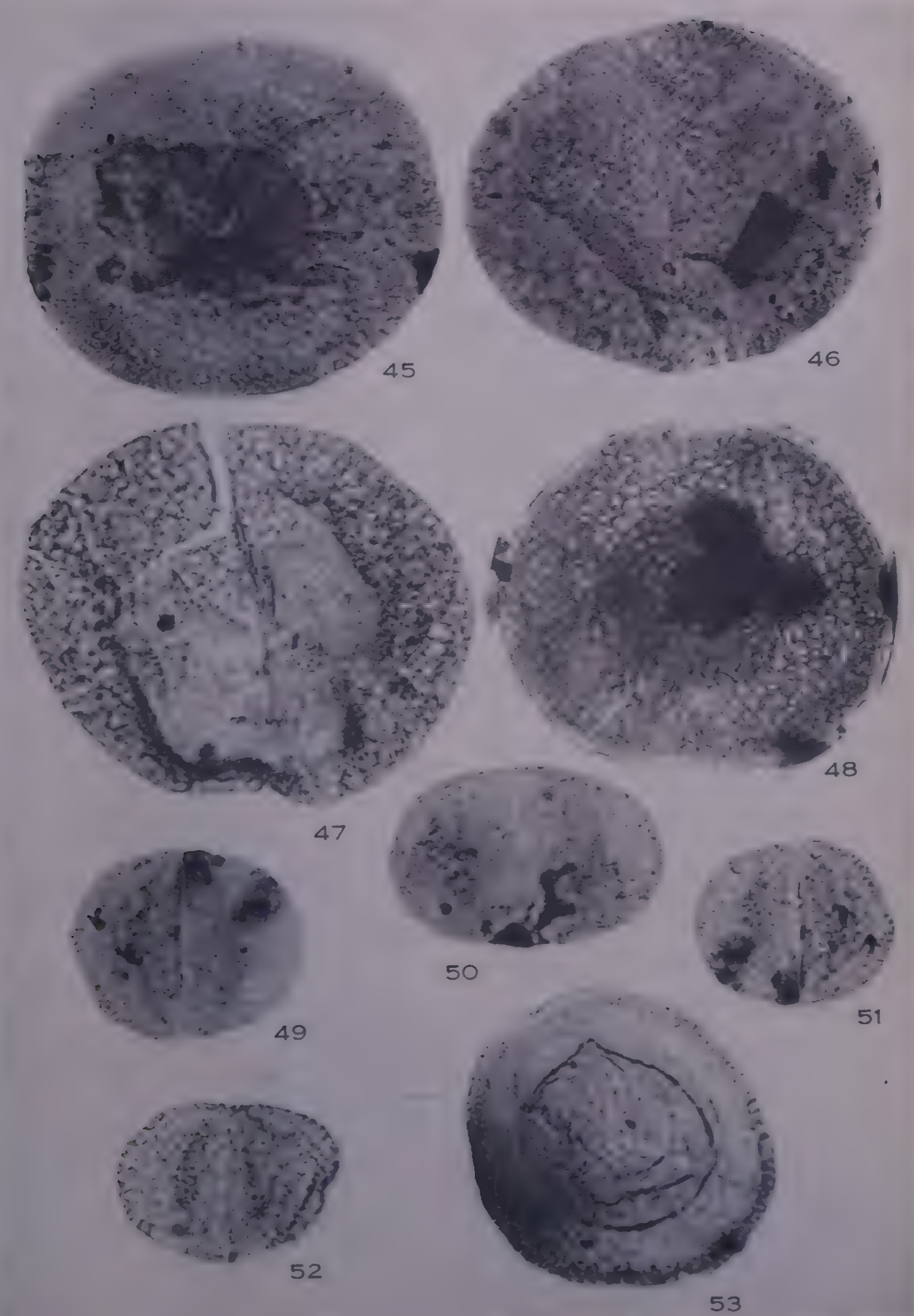

BISACCATE SPOROMORPHS

STUDIES IN THE ECOLOGY OF THE RIVERINE PLAIN

I. THE GILGAI MICRORELIEF AND ASSOCIATED FLORA

By O. B. Williams*

[*Manuscript received December 23, 1954*]

Summary

The flora of the gilgai microrelief at Deniliquin, N.S.W., is described, and the major vegetation changes over a 4-year period are outlined. Until 1950 the shelf was dominated by chenopodiaceous plants, the depression by perennial grasses, and the puff by annual grasses and herbs. After heavy and persistent winter rainfall in 1951, the depressions remained waterlogged for several months. The perennial grasses died out and were replaced by species of *Juncus* and *Carex* and *Eleocharis acuta* R.Br. With the return to more normal rainfall the earlier flora in the depression is being slowly re-established. From measurements made on the soils it would appear that physical factors are important in determining the species which grow on the shelf, depression, and puff respectively. Some of the factors concerned are: (*a*) the soil moisture content at which water becomes available to plants, and particularly to seeds; (*b*) the intensity of soil cracking, which influences seed retention, moisture penetration, and the extent to which root systems are damaged; (*c*) aeration of the soil.

I. Introduction

A conspicuous feature of the clay soils at Deniliquin, N.S.W., is the gilgai microrelief (described below), and its associated vegetation.

Observations were made on 12 acres of grassland with a perennial basal cover of 3 per cent. It had not been grazed for 5 years before the observations were commenced. Grassland of this type is used for extensive sheep raising in the Riverine Plain. The soil is a grey clay described by Butler and Johnston (1947) as soil type R. The three gilgai components occur in close proximity in the proportion of 40 per cent. shelf, 55 per cent. depression, and 5 per cent. puff.

This paper describes the vegetation and its relation to certain physical characteristics of the gilgai soils.

II. Climate

The mean annual rainfall at Deniliquin is 15.72 in. (87 years), 56 per cent. falling in the winter months April-September. The remainder consists of erratic thunderstorms in summer. The annual evaporation, as measured with a standard 36-in. diameter tank, is 63.6 in., and peak values in excess of 12 in. are recorded in January when precipitation is at its lowest. Rainfall and evaporation data for the period of observations are given in Table 1. It will be noted that the winter rainfall in 1951 exceeded 6 in. Temperatures exceed 100° F for short periods during summer, and a few heavy frosts occur during winter.

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III. Soil

The soil has a hummocky surface but three main levels may be distinguished. These are called the shelf, depression, and puff, and occur in variable proportions in gilgai areas.

The shelf component is commonly more extensive than either of the others. Its surface is massive and shows few cracks. These rarely exceed 0.5 cm in width. A grey or grey-brown clay loam 0.5-1 cm deep passes abruptly to a B_1 horizon of grey medium blocky clay with prismatic structure. In this horizon cracks are larger and more numerous. During summer, fissures may extend to a depth of 80 cm. Large crystals of gypsum occur at 80 cm and continue to at least 220 cm in the massive B-C horizon.

The depression is usually located between the shelf and the puff. It varies from 80 to 250 cm in width and lies as much as 10-20 cm below the level of the shelf. The surface structure is usually massive with occasional cracks, but in some cases the surface is closely dissected by cracks 5 cm wide and 5-10 cm deep. The B_1 horizon is similar to that of the shelf.

The puff component usually lies 30-50 cm above the level of the shelf. Its outcrops vary in shape and size from small mounds 250 cm in diameter to ridges 100 m long and 25 m wide. From the surface to 10 cm the structure is coarsely granular and self-mulching. The soil becomes massive at depth and at 50 cm the blocky structure typical of the B-C horizons of the other components can be discerned. Occasional limestone concretions are to be found at 40 cm and gypsum is present at 80 cm.

IV. Vegetation

(*a*) *Pre*-1951 *Species Distribution*

In 1949 and 1951 the density of all species on permanent quadrats 1 sq. m. in area was determined. The results for the three components are set out in Appendix I.

On those parts of the shelf where the surface is massive and unbroken a scattered population of perennial plants occurs. These include *Helichrysum apiculatum* DC., *Kochia aphylla* R.Br., *K. ciliata* F. Muell., *Leptorhynchus panaetioides* Benth., and *Stipa falcata* Hughes. They are accompanied in winter by the annual species *Goodenia pusilliflora* F. Muell., and various *Helipterum* spp., and in summer by *Chloris truncata* R.Br., *Sporobolus caroli* Mez, and *Eriochlamys behrii* Sond. Where the soil is cracked *Danthonia caespitosa* Gaudich. and *Medicago denticulata* Willd. are found. They characteristically occur along the edges of the cracks.

In the depression *Danthonia caespitosa* is the dominant species. It is accompanied by perennial herbs which include *Sida corrugata* Lindl., *Goodenia subintegra* F. Muell., and *Calotis scabiosifolia* Sond. & F. Muell., as well as annual herbs such as *Asperula conferta* Hook. f., *Calocephalus sonderi* F. Muell., and *Crassula colorata* Ostenf. *Medicago denticulata* is common along soil cracks. Annual grasses also occur in the depression. In winter *Vulpia myuros* (L.) Gmel. is prominent. In summer *Chloris truncata* and *Sporobolus caroli* occur. *Marsilea drummondii* R.Br. and *Juncus* spp. are occasionally found in depressions.

On the puff annual species are much more conspicuous than perennials. The few perennials which occur include *Bassia quinquecuspis* F. Muell., *Danthonia caespitosa*, *Kochia aphylla*, and *Sida trichopoda* F. Muell. The annual species occurring most often are the grasses *Avena fatua* L., *Bromus mollis* L., *B. rubens* L., *Hordeum leporinum* Link, and *Phalaris minor* Retz., and the herbs *Centaurea melitensis* L., *Daucus glochidiatus* (Labill.) Fisch., Mey. & Ave-Lall., *Hedypnois cretica* (L.) Willd., *Medicago denticulata*, and *M. tribuloides* Desr.

Similar patterns in vegetation distribution are described by Leeper, Nicholls, and Wadham (1936) and Tiver and Crocker (1951) in 20-in. rainfall country. They have also been observed in desert gilgai with an annual rainfall of 7-8 in. by Crocker and Skewes (1941) and by Crocker (1946).

An important difference has been noted between the annual plants characteristic of the shelf and those which grow on the puff or other areas subject to cracking. The annual plants of the massive parts of the shelf are mostly small-seeded while those of areas subjected to cracking are large-seeded. An important exception is *Goodenia pusilliflora*, the large seed of which adheres to the soil surface by a gelatinous margin. Plants such as *Avena fatua* and *Sonchus oleraceus* L. are dominant on the puffs because their large fruits or seeds lodge in the granular surface soil. Small seeds drop down the cracks and seeds of *Plantago varia* R.Br. have been recovered from soil at 10-25 cm depth. A further advantage held by species with large fruits is their capacity to keep the germinating seed in a favourable environment if the loose surface soils temporarily dry out. On massive parts of the shelf the small-seeded plants have a greater chance of survival than large-seeded plants because minor irregularities in the soil surface provide a good seed bed. Winds move large fruits into fissured areas where they are retained. Taken together these factors tend to limit species with large fruits to fissured areas whether depression or puff, and small-seeded species to massive soils.

The plants of each of the gilgai components show important differences in root development. On the shelf, species like *Leptorhynchus panaetioides* and *Helichrysum apiculatum* have a well-developed layer of small roots in the surface soil. Several thick roots with secondary thickening descend into the subsoil. Robust suberized roots are characteristic of *Kochia aphylla* and *K. ciliata*. Moisture is used during rainless periods in the tap-roots of *K. ciliata*. In *K. aphylla* there are few roots in the surface soil. However, the primary root system is very well developed. The main roots of all four species can withstand considerable shearing forces and follow cleavage planes in the subsoil. The occasional root hairs on them penetrate the smaller cracks but leave most of the soil mass untouched. The distribution of roots in the soil enables the plants to benefit from light showers which wet the surface horizon, and intensive rains which infiltrate to the subsoil. The geophyte members of the community, including *Anguillaria dioca* R.Br. and *Hypoxis pusilla* Hook f., are of especial interest as they respond only to heavy and consistent rainfall because their perennating organs are 2-4 cm below the surface. On the puff component *Sida trichopoda* and *Bassia quinquecuspis* develop root systems similar to that of *K. aphylla*. Several annual and biennial species develop a strong tap-root. These include *Centaurea melitensis* L., *Carthamus lanatus* L.,

Sonchus oleraceus, and *Hypochoeris radicata* L. In these species there is a marked absence of an extensive root system in the surface soil of the puff. In the depression very few species have specialized root systems. *Danthonia caespitosa* and its associated herbs thoroughly explore the surface horizon and the upper parts of the subsoil. In general the deeper roots follow cleavage planes, but their root hair development is better than that of any species in either the shelf or puff.

(*b*) *Alterations in Vegetation Pattern after the* 1951 *Winter*

The rainfall in the winter of 1951 was abnormally high. Details of rainfall and evaporation for 1948-50 and 1952 are compared with those of 1951 in Table 1.

TABLE 1

RAINFALL AND EVAPORATION (IN.), DENILIQUIN, 1948-52

Climatic Data	1948	1949	1950	1951	1952	Mean (87 yr)
Rainfall:						
Annual	16.08	13.42	20.76	14.43	18.43	15.72
June-Aug.	3.23	1.34	3.02	6.31	2.59	4.49
June-Aug., wet days	30	19	26	40	33	
Evaporation:						
Annual	—	62.50	61.90	66.80	62.00	
June-Aug.	—	5.90	4.50	4.20	4.70	

It will be noted that although the rainfall for 1951 was low, 6.31 in. (or 43.7 per cent.) fell in 3 months when evaporation from a free water surface was only 4.20 in. Wet winters of this type occur on an average every 8-10 years, and waterlog the depressions and low-lying areas in the shelf component for several months. In response to these conditions the perennial flora of the depressions showed considerable alteration. Less drastic changes occurred on the shelf and puff.

Danthonia caespitosa was replaced in depressions and low-lying areas of shelf by species which are characteristic of semi-permanent swamps. These included *Eleocharis acuta* R.Br., *Marsilea drummondii*, *Carex* spp., and *Juncus* spp. *Wahlenbergia gracilis* (Forst. f.) A.DC., *Centaurium spicatum* (L.) Druce, and *Centipeda cunninghamii* (DC.) A.Br. & Aschers. were recorded in depressions for the first time. Various liliaceous plants, characteristic of a mesic habitat, were noted on the shelf. These included *Arthropodium minus* R.Br., *Bulbine bulbosa* (R.Br.) Haw., *Dichopogon strictus* (R.Br.) J. & G. Bak., and *Thysanotus* sp. *Calocephalus sonderi* and *Crassula colorata*, which were common in depressions in previous seasons, now grew vigorously on the shelf. A hydromorphic community had developed on the

depressions from dormant rhizomes, and there was some migration of species usually characteristic of the depressions onto the shelf and puff.

Figure 1 is a schematic diagram illustrating the change in distribution of the flora on the gilgai soils with heavy and prolonged winter rain.

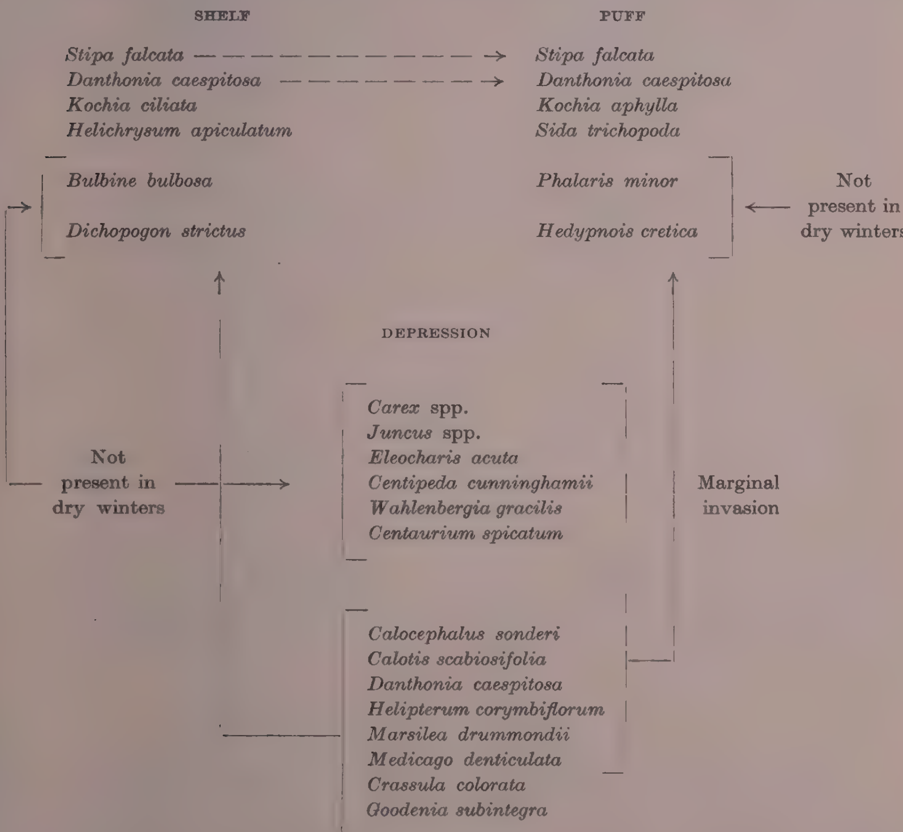

Fig. 1.—Schematic diagram of the floristic change in the gilgai microrelief from dry to wet winters. — → Denotes partial removal by wet conditions in low-lying areas.

In 1951 the density of both annuals and perennials on the puff was higher than in the preceding years. In addition, the individual plants were larger. Results from plant density determinations on permanent quadrats in December 1951 are set out in Appendix I. The basal area of perennial grasses in December 1949, 1951, and 1952 is set out in Table 2.

The wet conditions were responsible for a heavy reduction in the basal area of perennial grasses on all soils. This change was more prolonged in its after-effects than the 2-year drought period 1944-45, from which a complete recovery was made by late 1947. This may be due in part to competition from the increased number of annual grasses and herbs in the depression and puff (Appendix I).

On these gilgai, waterlogging seldom occurs more often than once in 8 years and there are considerable changes in vegetation pattern. On gilgai which pastoralists irrigate annually by "wild flooding" the plant communities are more stable. The depression is dominated by swamp plants, including *Juncus* spp., *Cyperus* spp., and *Carex* spp., the shelf by *Calocephalus sonderi* in winter and *Chloris truncata* in summer, and the puff by *Stipa falcata*. The circumference of the puff is occupied exclusively by *Danthonia caespitosa*. *Medicago tribuloides*, a more mesomorphic species than *M. denticulata*, is the associated herb in winter.

Table 2

BASAL AREA OF PERENNIAL GRASSES BEFORE AND AFTER THE 1951 "WET" WINTER (PER CENT.)

Component	1949	1951	1952
Shelf	2.32	0.10	0.35
Depression	3.80	0.54	0.39
Puff	1.27	0.01	0.02

From the observations made during 1948-52 it appears that physical differences between the three soils at 0-8 cm depth affect the distribution of plant species. The factors selected for study were: (*a*) the ability of the soils to supply water to plants; (*b*) amount of surface cracking; (*c*) aeration. Therefore the following studies were made.

V. Experimental Procedure

Moisture tension curves were constructed by the method of Gardner (1937) as outlined by Leeper (1952). These curves were used for the determination of wilting point. The osmotic term of soil moisture stress was assessed by assuming that all chlorides in the soil were sodium chloride, and that all chlorides were in solution at the wilting point. The contribution of the osmotic term at the wilting point was 0.8, 0.6, and 0.2 atm for the shelf, depression, and puff respectively.

Soil moisture percentages were measured at fortnightly intervals during 1951-52, and available moisture for plant growth was calculated as the difference between the field maximum and wilting point. Field capacity was not measured since there is no unique value of field capacity in soils with poor internal drainage (Richards and Wadleigh 1952).

Bulk density was obtained for a range of soil moisture by the method of Coile (1936), and the density of clods weighing 20-35 g by the method of Johnston (1945). Particle or absolute density was determined by a displacement method using toluene.

VI. Results

(a) *Soil Moisture Relations*

Figure 2 shows the curves of soil moisture against tension for the 0-8 cm depth of the three gilgai components. At the wilting point (pF 4.2) the soil moisture content ranged from 12 per cent. in the shelf to 22 per cent. in the puff. These values were confirmed by soil sampling when seedling plants wilted in the field.

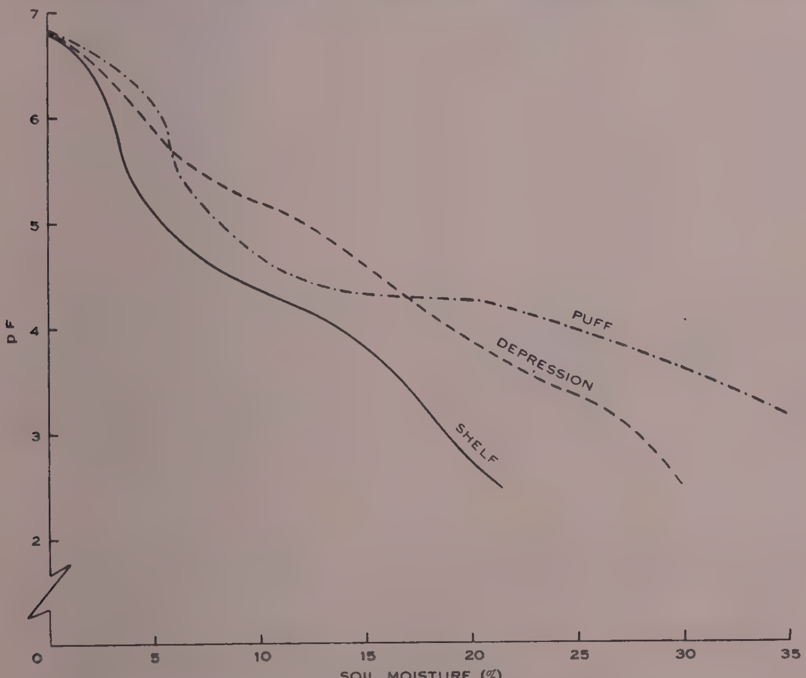

Fig. 2.—The pF of soil water in the three components of the gilgai microrelief.

In Table 3 the wilting point, and the maximum field value for the soil moisture recorded in the period 1951-52, are set out.

Before the volume of available moisture in each component can be assessed, the bulk densities of the soil at wilting point and at maximum soil moisture must be determined because all three soils contract on drying and swell on wetting. Regressions of bulk density on soil moisture are set out in Table 4.

To moisten the 0-1 cm depth of these soils from midsummer values of soil moisture to the wilting point it has been calculated that 0.11 cm of water is required by the shelf, 0.16 cm by the depression, and 0.13 cm by the puff. After light rain seeds germinate on the shelf first and on the depression last.

To moisten the 0-8 cm depth of these soils from midsummer values of soil moisture to the maximum recorded during 1951-52 it has been calculated that 2.25

cm of water is required by the shelf, 2.60 cm by the depression, and 1.86 cm by the puff. But these amounts of rain would not be absorbed by the shelf and depression unless they fell as intermittent light showers. This seldom happens. Heavy rain is of much more common occurrence. Once it has saturated the top 2 or 3 centi-

TABLE 3

SOIL MOISTURE VALUES FOR THE GILGAI MICRORELIEF (PER CENT.)

All values are for the 0-8 cm depth

Soil Moisture Value	Shelf	Depression	Puff
Wilting point	12.0	17.5	22.0
Maximum soil moisture, 1951-52	26.4	34.5	35.8

metres of the soil, the rate of absorption of the water by the soil is reduced. Run-off then starts and the surplus water drains down cracks to create pockets of saturated subsoil 20-8000 c.c. in volume. Some rain runs off into depressions. This does not happen in the puff because it is very permeable. The highest reserve of available soil moisture for the 0-8 cm depth was 1.35 cm for the shelf and depression but only 0.86 cm for the puff.

TABLE 4

REGRESSION* OF BULK DENSITY ON SOIL MOISTURE

Component	Depth (cm)	a	b
Shelf	0–8	1.452	0.0061
Depression	0–8	1.444	0.0071
Puff	0–8	1.309	0.0095

* Regression, $y = a - bx$, where y = bulk density and x = soil moisture (%).

The shelf is the most massive component at each moisture level, and the degree of swelling is greatest for the puff. In general the greater the volume change in a soil the more cracking occurs at the surface. The puff cracks most, the shelf least. This cracking of the soil may influence plant distribution by breaking roots. It also has an effect on seed dispersal. Small seeds tend to fall so far down cracks that seedlings are unlikely to establish successfully. Large seeds tend to be retained near the surface where chances of establishment are good.

(*b*) *Aeration*

In clay soils which swell and contract, bulk density samples give misleading results because they include wide cracks which have little effect on aeration within the clods. On this account individual clods were taken for study, and the results of density determinations in relation to soil moisture are shown in Table 5.

The puff clods are dense at low moisture values but swell so strongly on wetting that the density falls below unity. Clods from the shelf (0-1 cm) and from the depression (0-8 cm) show only a slight volume reduction with increasing soil moisture.

TABLE 5

REGRESSION* OF CLOD DENSITY ON SOIL MOISTURE

Component	Depth (cm)	a	b	c
Shelf	0–1	1.517	0.0062	
	1–8	1.514	0.0094	
Depression	0–8	1.510	0.0077	
Puff	0–8	1.722	0.0383	0.0006

* Regression for shelf and depression, $y = a - bx$; for puff, $y = a - bx + cx^2$; where y = clod density and x = soil moisture (%).

In order to obtain an estimate of air space in each of the soils, the particle density (g/c.c.) was determined for each component. The values were found to be 2.60 for the shelf, 2.61 for the depression, and 2.67 for the puff. The high value found for the puff is probably due to the presence of limestone concretions. The air space available for aeration in clods of each of the three components at moisture values corresponding to the wilting point and maximum soil moisture observed, is shown in Table 6.

At the maximum soil moisture there is little air space in the depression soils. Air space figures as low as 1.3 per cent. have been obtained in some areas of this component. In the 0-1 cm depth of the shelf 3.5 per cent. has been recorded. It is probable that poor aeration will alter the flora of the depression and, under very wet conditions, that of the shelf as well.

VII. DISCUSSION

Earlier workers have given accounts of the vegetation of gilgai soils and have reported that some species are confined to a particular soil component or reach their maximum development there.

The vegetation of the gilgai of the Riverine Plain also follows a pattern determined by that of the soils, but the vegetation pattern is not static. It is in dynamic equilibrium with its environment. The species concerned have distributions fluctuating in response to current rainfall.

Under average rainfall the factors controlling the distribution of plants on the shelf are:

(1) Low wilting point.

(2) Few cracks and surface sealing.

Light rainfall makes water available in the surface soil for plant growth. Run-off occurs at an early stage because the surface is sealed by the swelling of the colloids and the reduction in the number of large pores. Perhaps the beating of raindrops (cf. Crocker 1946) helps this dispersal. Run-off water either enters the few cracks and creates pockets of wet soil in the subsoil, or it floods the nearby depressions. Lack of cracking favours perennial plants. Annual plants with small seeds occur frequently because they find suitable niches for germination in minor irregularities of the surface soil.

TABLE 6

VOLUME OF CLODS OCCUPIED BY SOIL, WATER, AND AIR (PER CENT.) AT WILTING POINT AND MAXIMUM SOIL MOISTURE

Component	Depth (cm)	Wilting Point		Maximum Soil Moisture
Shelf	0–1	Soil	55.0	52.7
		Water	20.4	33.7
		Air	24.6	13.6
	1–8	Soil	49.6	49.2
		Water	27.3	34.3
		Air	23.1	16.5
Depression	0–8	Soil	52.2	56.3
		Water	26.9	38.2
		Air	20.9	5.5
Puff	0–8	Soil	43.4	39.7
		Water	24.4	35.0
		Air	32.2	25.3

The factors controlling the distribution of plants in the depression are:

(1) Extra water running off the shelf.

(2) Water standing in depressions and soaking in, in spite of surface sealing.

(3) Severe cracking found in some depressions, which assists water penetration but damages the root systems of perennial plants.

(4) Inadequate air space in the depression.

Mesomorphic and hydromorphic species occur in the depression because the soil moisture regime favours them. Ephemeral species, some of them common on the shelf, may develop in uncracked depressions after light rainfall. Perennial

plants such as *Danthonia caespitosa* do not occur in severely cracked areas. They are replaced by annual species with large fruits (*Medicago denticulata*) or large fruiting inflorescences (*Hedypnois cretica*, *Sonchus oleraceus*). These are retained near the surface in large cracks. Few of the species normally conspicuous in depressions survive long periods of waterlogging of the soil. Once they die out they are replaced by species of *Juncus* and *Carex*.

The factors controlling the distribution of plants in the puff are:

(1) Intensive cracking.

(2) Ready absorption and even penetration of rain water.

(3) Rapid drying of the surface soil.

(4) High wilting point.

Perennial plants with spreading root systems do not find favourable conditions on the puff. The soil cracks so severely that root systems are mutilated. The perennials that do grow have reinforced roots which withstand these forces.

Annual plants with small seeds are discriminated against because the seeds fall down cracks. Annual plants with large seeds or fruits find conditions favourable on the puff because they lodge in large cracks near the surface. In addition the germinating seeds are kept in a moist environment should the soil temporarily dry out. Heavy rainfall is needed before a vigorous plant community will develop on the puff, because the surface soil transmits water readily to the subsoil and the wilting point is high. This plant community consists largely of deep-rooted perennial or biennial species and of annual plants with large seeds. These annual plants complete their life cycle before the soil dries and cracks. With excessively heavy rainfall the puff provides a mesic environment for plants, and with average to below average rainfall it is a xeric environment.

Since the perennial grasses of the gilgai recover more rapidly from drought than from the effects of flooding it is possible that the vegetation shows greater adaptation to a dry environment than it does to a wet one. This adaptation may be indicated by the abundance of short-lived annuals in the area. These complete their life cycles in the brief periods during which the environment is favourable. Under one set of environmental conditions a certain plant species may be limited to a specific gilgai component. Should these conditions change it is possible that this species may occur exclusively on another component. The migration and demarcation of the flora on gilgai soils appear to reflect environmental fluctuations to an extent not usually observed on uniform soils.

VIII. Acknowledgments

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Appendix I

DENSITY OF PLANT SPECIES IN AN AREA OF GILGAI MICRORELIEF IN 1949 AND 1951 ON PERMANENT QUADRATS (PER METRE SQUARE)

Species	Shelf		Depression		Puff	
	1949	1951	1949	1951	1949	1951
PERENNIALS						
GRASSES						
Chloris acïcularis Lindl.	1	1	*T**	—	—	—
Stipa falcata Hughes	2	—	*T*	—	—	—
Danthonia caespitosa Gaudich.	42	—	24	3	9	—
Agropyron scabrum (Labill.) Beauv.	—	—	—	*T*	—	—
Panicum prolutum F. Muell.	—	—	—	—	1	—
	45	1	24	3	10	—
RUSHES AND SEDGES						
Juncus spp.	—	—	—	1	—	—
Carex spp.	—	—	—	5	—	—
	—	—	—	6	—	—
HERBS						
Hypoxis pusilla Hook. f.	—	6	7	—	—	—
Dichopogon strictus (R.Br.) J. G. Bak.	—	*T*	—	—	—	—
Teucrium racemosum R.Br.	1	—	—	—	—	—
Goodenia subintegra F. Muell.	3	12	1	4	—	—
Wahlenbergia gracilis (Forst. f.) A.DC.	—	1	2	6	—	—
Kochia excavata J. M. Black	1	1	—	—	—	—
Kochia ciliata F. Muell.	71	33	3	*T*	*T*	—
Atriplex semibaccata R.Br.	1	—	2	—	*T*	—
Bassia quinquecuspis var. *villosa* F. Muell.	—	—	2	—	4	—
Marsilea drummondii R.Br.	—	—	—	3	—	—
Sida corrugata Lindl.	1	—	1	—	1	1
Sida trichopoda F. Muell.	—	—	1	—	4	—
Helichrysum apiculatum (Labill.) DC.	1	1	—	—	—	—
	79	54	19	13	9	1

* T, trace

Appendix I (*Continued*)

Species	Shelf		Depression		Puff	
	1949	1951	1949	1951	1949	1951
ANNUALS						
GRASSES						
Chloris truncata R.Br.	4	—	4	—	*T*	—
Sporobolus caroli Mez	10	*T*	9	—	—	—
Vulpia myuros (L.) Gmel.	—	—	3	34	—	—
Parapholis incurva (L.) C. E. Hubb.	—	—	1	1	—	1
Eragrostis parviflora (R.Br.) Trin. (1931)	—	—	—	1	—	—
Bromus mollis L.	—	—	—	7	1	38
Bromus rubens L.	—	—	—	1	—	1
Phalaris minor Retz.	—	—	—	—	1	45
Hordeum leporinum Link	—	—	3	5	—	1
	14	*T*	20	49	2	86
HERBS						
Eriochlamys behrii Sond.	98	61	—	—	—	—
Isoetopsis graminifolia Turcz.	—	1	—	—	—	—
Helipterum albicans (A. Cunn.) DC.	—	5	—	—	—	—
Goodenia pusilliflora F. Muell.	12	19	—	—	—	—
Plantago varia R.Br.	—	8	—	12	—	—
Matricaria discoides DC.	—	3	1	2	—	—
Crassula colorata Ostenf.	—	10	—	30	—	—
Calocephalus sonderi F. Muell.	1	38	41	25	2	1
Medicago denticulata Willd.	—	3	3	9	3	9
Daucus glochidiatus (Labill.) Fisch., Mey. & Ave-Lall.	*T*	2	5	3	1	2
Sonchus oleraceus L.	—	—	—	7	—	3
Euphorbia drummondii Boiss.	*T*	—	—	—	*T*	—
Asperula conferta Hook. f.	—	—	6	3	—	—
Helipterum corymbiflorum Schlecht.	—	2	6	8	—	1
Trifolium glomeratum L.	—	—	—	1	—	—
Alternanthera denticulata R.Br.	—	—	1	—	—	—
Erodium cicutarium (L.) L'Hérit.	—	1	1	1	—	*T*
Hedypnois cretica (L.) Willd.	—	—	—	1	3	14
Trifolium suffocatum L.	—	—	—	*T*	—	1
	111	153	64	102	9	31
TOTAL	249	208	127	173	30	118

DISTRIBUTION AND ECOLOGY OF THE GENUS *KENNEDYA* VENT. IN WESTERN AUSTRALIA

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Summary

A review of the taxonomy, ecology, and distribution pattern of 11 species of the genus *Kennedya* Vent. in relation to the soils and climate of Western Australia is presented. Within a single climatic zone the edaphic factor is shown to be the most important, but it is also shown that "growing period" calculated from $P/E_w{}^{0.75}$ values can be useful in delineating the climatic requirements of some endemic species.

Variability and distribution are discussed in relation to the above factors, the occurrence of self-fertilization, and the influence of previous climates.

Introduction

The development of pasture legumes adapted to the climatic and edaphic conditions of the wheat belt of Western Australia is recognized as one of the most pressing problems confronting agriculturalists in this State. In a large proportion of the wheat-belt areas no suitable legume is available for cultivation, since the 14-in. isohyet at present limits the inland extension of subterranean clover (*Trifolium subterraneum* L.), the most extensively cultivated pasture species in Western Australia.

There are three main ways in which the desired type of legume may be obtained:

(i) Selection of earlier-maturing and more drought-resistant strains from existing species;

(ii) Introduction of exotics;

(iii) Use of native species.

Davies (1951) has drawn attention to the fact that exploitation of the rich store of species and gene complexes which constitutes our native flora has not been seriously attempted. He recommends the initiation of long-term studies of the agronomic and ecological characteristics of selected genera or species with a view to their development for agricultural purposes.

The advantages of using such groups are fairly evident. They fulfil certain requirements in regard to adaptability, and are readily accessible.

Species of the genus *Kennedya* are extensively developed in certain localities in Western Australia, showing an inherent ability to produce good growth on soils low in plant nutrients. All are herbaceous or woody perennials with well-developed root nodules. These facts make the group worthy of investigation to assess their suitability for agricultural purposes.

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The study reported in this paper represents a general morphological, distributional, and ecological survey of all Western Australian species of *Kennedya* in relation to climate, major vegetation formations, and soil groups. Field observations, supported by transplantation and cultivation under uniform conditions, have demonstrated the existence of ecotypes. Information of agronomic and genetic significance has thus been acquired and provides a basis for the understanding of the evolutionary history of the genus.

Physiographic and Geological Background

Since all except one of the species of *Kennedya* known to occur in Western Australia are found within the South-West Province (Gardner 1942), discussion will be almost entirely limited to this area, which extends south-west of a line drawn from the mouth of the Murchison River in the north to Israelite Bay in the south. It is also known as the "South Western Agricultural Region" (Smith 1952).

Only a brief outline of the physiography and geology will be given here. For more detailed accounts the reader is referred to Jutson (1934), Gardner (1942), Clarke, Prider, and Teichert (1944), and Smith (1952).

The area forms part of an ancient plain elevated to an average height of 1000-1500 ft, the surface of which is mostly flat or gently undulating. There is evidence of more active erosion than in the present, relatively arid cycle. Pre-Cambrian rocks form the major part of the basement strata. These are fringed along the west and part of the south coast by sediments of Quaternary age. Miocene sediments known as the Plantagenet series extend along the south coast from Albany to Hopetoun. Further Miocene deposits occur east of Esperance.

The general features of the region indicate a prolonged period of geological stability. This fact, together with a considerable degree of climatic stability, is reflected in the character of the vegetation and soils.

General Features of Climate and Soils

(*a*) *Climate*

The climate of the region is generally described as mediterranean, being characterized by a predominantly winter rainfall followed by a marked summer drought which decreases in intensity from north to south. The rainfall figures for Geraldton, Perth, and Albany (Table 1) indicate this trend.

The average annual rainfall varies from 10 in. on the north and east boundaries of the region to above 50 in. in the extreme south-west. Rainfall variability expressed as percentage departure from the mean is for the most part less than 20 per cent. (Gardner 1942). Mean temperatures range from 66-77°F for January, the hottest month, to less than 50-55° for July.

Prescott (1938, 1949*a*) and Prescott, Collins, and Shirpurkar (1952) have considered the usefulness in Australia of adaptations of the Meyer and Transeau ratios as climatic indices in relation to plant growth. It is found that the length of the growing season can be expressed by the period during which the value for $P/E_w^{0.75}$ (where P = precipitation and E_w = evaporation from a free water surface)

TABLE 1

MEAN MONTHLY RAINFALL AT THREE SELECTED STATIONS

Upper rows of numbers give mean rainfall in inches; lower rows monthly percentage of total annual rainfall

Station	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Geraldton (64 yr)	0.22	0.29	0.57	0.92	2.72	4.77	3.79	2.79	1.28	0.70	0.26	0.15	18.46
	0.8	1.7	3.1	5.0	14.7	25.8	20.5	15.1	7.0	3.8	1.4	0.8	
Perth (66 yr)	0.33	0.40	0.81	1.71	5.05	7.09	6.72	5.71	3.36	2.19	0.76	0.54	34.67
	0.9	1.2	2.3	4.9	14.5	20.4	19.4	16.5	9.7	6.3	2.1	1.6	
Albany (65 yr)	1.01	0.88	1.59	2.75	5.02	5.43	5.59	5.30	4.08	3.24	1.46	1.15	37.50
	2.7	2.3	4.2	7.3	13.3	14.5	15.0	14.1	10.8	8.6	3.9	3.1	

exceeds 0.4, if temperature is not limiting, since evapotranspiration (E_{tr}) can be related to evaporation from a free water surface (E_w) by the equations

$$E_{tr}/E_w^{0.68} = 1.33$$

and

$$E_{tr}/E_w^{0.79} = 1.50.$$

Maps showing the length of the growing period based on monthly calculations of the above index can be prepared. Where no month has a value of 0.4, desert

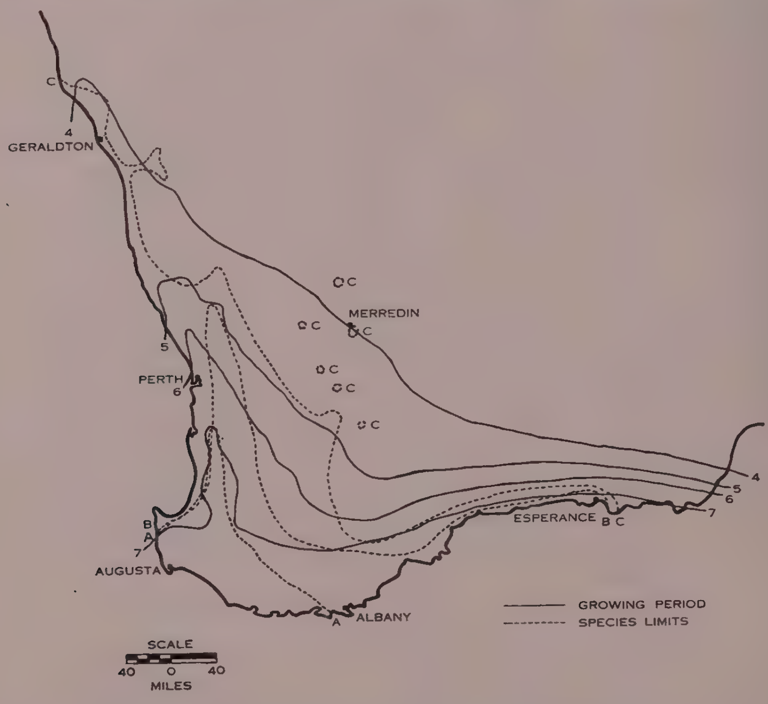

Fig. 1.—Map of the South-West Region of Western Australia, showing limits of the 4-, 5-, 6-, and 7-month growing periods and distributional limits of *K. carinata* (Benth.) Domin (*A*), *K. coccinea* Vent. (*B*), and *K. prostrata* R. Br. (*C*). Distributions are overlapping, i.e. line *A-A* includes both *K. coccinea* and *K. prostrata* as well as *K. carinata*.

conditions prevail; a minimum of 5 months is required for seasonal cropping, and 9 months for perennial pastures resistant to drought. Prescott (1949*b*) has given a value of $P/E_w^{0.75}$ greater than 0.54 for the commencement and maintenance of growth after break of drought. This latter value has been used as a climatic index in relation to *Kennedya* distribution (see Fig. 1) in view of the fact that growing period maps of the South-West Province have been prepared from it by the Commonwealth Meteorological Bureau.

The relationships obtained by Prescott between evapotranspiration and evaporation from a free water surface have been derived from studies on economic plants. It is likely that *Kennedya* species have a lower rate of transpiration than cultivated crops, in which case they would have a longer growing period than that indicated by the limits shown in Figure 1.

The application of this concept of the determination of the efficiency of the rainfall in any month by reference to both precipitation and evaporation in that month gives a more intelligible picture of the climate of an area than that obtained by the presentation of rainfall and temperature data only.

(*b*) *Soils*

The soils of Western Australia were first described and classified by Prescott (1931), who recognized six major zones but later (1944) expanded these to 15. Teakle (1938) described nine zones and 33 regions. More recently Smith (1952) has reviewed the work of these authors and presented a much more detailed account of the soils of the South-West Agricultural Region. He suggested that the complex soil pattern of this area falls into two zones which can be defined in terms of the dominant profiles as:

(i) The zone of podzols, laterites, and south-western brown soils; this zone embraces the podzol zone and most of the red-brown earth zone of Teakle and Prescott.

(ii) The zone of sandy laterites and pedocals.

Lateritic formations dominate the soil pattern and occupy at least three-quarters of the total area (Smith 1952). Formation of lateritic soil has been the subject of some controversy but it is now generally agreed that evidence favours a pedogenic origin (Stephens 1946). The nature of a lateritic profile is described by Stephens as essentially a podzol, consisting of A, B, and C horizons of eluviation, illuviation, and weathering, with an accessory laterite horizon usually, but not invariably, situated on top of the clayey B horizon. The nature and relationship of the soils formed as a result of dissection of this fossil soil are also discussed by this author and are illustrated in diagram form. Two groups of soils are recognized, viz. soils formed on exposed materials and on transported materials respectively.

A summary of the relationship of soils to the fossil profile, as a result of truncation, is as follows (after Holland 1952).

Soil Types	Fossil Profile
(*A*) Sands	A_1 and A_2
(*B*) Gravelly sands—e.g. sand plains	A_2
(*C*) Laterite—lateritic residuals of W.A. sand plains	Laterite
(*D*) Kaolinitic clays	

Regions of Kennedya Distribution

The distribution of species of *Kennedya* in Western Australia can be related to several natural zones or regions. These are based largely on the appropriate soil regions of Teakle (1938) and the soil combinations of Smith (1952), but in some

cases it has been necessary to select only a single feature or aspect of an area where that feature or aspect clearly has an influence on the distribution pattern. A brief description of the 12 distinguishable zones follows. These are shown in Figure 2.

(1) *North Coastal*.—This is a narrow coastal strip from Dongarra to Lynton Station and constitutes the northern part of the Boranup combination. The area consists entirely of coastal sand dunes of Pleistocene age, many alkaline and most containing concretionary calcium carbonate in the A and B horizons. The vegetation is the typical maritime dune formation. The average annual rainfall is 18 in., with a 90 per cent. winter incidence.

Fig. 2.—Map of the South-West Region of Western Australia, showing regions of *Kennedya* distribution. Regions 1-12 are as defined in the text.

(2) *North Subcoastal*.—Two areas, the Northampton combination and the drainage basin of the Irwin River, are combined under this heading but in actual fact are separated by a wide strip of sand plain country of distinctive characteristics on which *Kennedya* does not occur. The soils are mostly brown and red-brown sands and loams, with mottled sandy clay subsoil formed over gneissic rocks or brown sandy loams over sandstones. These soils are related to the south-western brown soils (red-brown earths) more extensively developed in the Avon valley. The topography is gently to steeply undulating, sedimentary rocks of Jurassic sandstones capped by laterite frequently constituting mesas. Savannah woodland forms

the major vegetative formation, with York gum (*Eucalyptus loxophleba* Benth.) and jam (*Acacia acuminata* Benth.) as dominants. The average annual rainfall is 16-18 in. with an 80-90 per cent. winter incidence.

(3) *Swan Littoral.*—The Swan Coastal Plain lies between the coast and the Darling Scarp (distance 10-25 miles), extending for about 170 miles from north of Bullsbrook to the vicinity of Busselton in the south. The soil pattern presents a complex of alluvium deposits, and sand separated from Pleistocene aeolinite by the agencies of water and wind. Near the foot of the Scarp gravel is frequently incorporated. The alluvium soils have a sandy surface (pH 6.0-6.9) and are underlain by clays and sandy clays, whereas the sands are characterized by a grey surface (pH 6.0) with which organic matter is incorporated, over deep ($>$ 20 ft) grey-white or yellow sand of pH about 6.5.

The Boranup combination of sand dunes and sand over limestone is encountered near the coast.

The rainfall is about 35-40 in. and the vegetation (apart from dunes) sclerophyll forest with an understory of sclerophyll shrubs.

(4) *Darling.*—This region, on the western edge of the Great Plateau, is essentially a dissected peneplain of average elevation about 1000 ft. Here and in the two regions to the south (regions 5 and 6) the old peneplain Pliocene soils have been truncated to varying degrees as described by Stephens (1946). Frequently erosion of the laterized surface has resulted in disintegration into a ferruginous gravel. Soils may be generally described as lateritic, the surface being a yellowish grey sand to sandy loam, or a grey sand with or without gravel. Subsoils generally consist of a yellowish clay, which is often gravelly. Massive laterite formations are common.

In the valleys where the underlying country rock is frequently exposed, shallow stony soils are forming under the present cycle of erosion.

The vegetation is the Jarrah Forest of Gardner (1942), dominated by jarrah (*Eucalyptus marginata* Sm.) and marri (*E. calophylla* R. Br.). To the east, at about the 25-in. rainfall isohyet, the jarrah is partly replaced by wandoo (*E. redunca* var. *elata* Benth.). The rainfall reaches a maximum of 50 in. on the crest of the Darling Scarp near Dwellingup but falls to 20 in. on the drier inland margins.

(5) *Chapman.*—In the extreme south-western portion of the State the Darling Scarp continues southward through Donnybrook and Nannup, but in this area does not descend to a coastal plain but to a low plateau of average elevation 300 ft. The terrain is gently undulating and timbered predominantly by the jarrah-marri forest. Bull banksia (*Banksia grandis* Willd.) and sheoak (*Casuarina*) and areas of heath are associated with sand formations. The soils are mostly sandy loams or loams with admixture of gravel derived from sandy clay representing material of alluvial and colluvial origin which has been extensively laterized. The rainfall is 35-45 in.

(6) *Nornalup.*—The Pre-Cambrian plateau here is deeply dissected and there are many sloping areas where the country rock is exposed at the surface. Detailed soil surveys within this region have been reported by Hosking and Burvill (1938)

and Smith (1951). Two major groups of soils are recognized—the Wakundup and the Kwilalup associations. Within the former the dominant soil above the 450-ft contour is the Wakundup series of weakly podzolized sands to sandy loams overlying yellow to light yellow-brown clay subsoils. It is on this soil that karri (*E. diversicolor* F. Muell.) reaches its best development in the south-western part. Jarrah and marri are predominantly associated with the Kwilalup association, the pattern of the old sandy soils found on level to gently undulating country at the higher or lower levels. The dominant soils are Kordabup and Kwilalup sands (Smith 1951). The rainfall is between 35 and 60 in.

(7) *Narrikup.*—South of the Porongorup Range, and between the Hay River in the west and Mt. Manypeak in the east, lies the poorly drained lowland of the Albany-Narrikup district. The Plantagenet series of Miocene sediments which underlie most of the area are dissected to a gently undulating land surface between sea-level and 500 ft. The drainage is generally senile, with the result that there are many depressions which are either permanently wet or where the water-table persists close to the surface for the major part of the year. Laterite is widespread, the dominant soils being sands or gravelly sands over gravelly clays.

The rainfall varies from 30 to 40 in. and the vegetation is dominated by stunted jarrah and marri. This region marks the easternmost limit of the Jarrah Forest.

(8) *South Coastal.*—East of the Narrikup region and south of the Stirling Range, a strip of scrub-covered, very gently undulating plain extends eastward beyond Esperance to Israelite Bay. This comprises the Woogenilup and Esperance Downs combinations of Smith (1952) and the Eyre region of Teakle (1938). Parent materials are predominantly Miocene sediments over the western part (Woogenilup) and Pre-Cambrian rocks over the eastern (Esperance) half. The strip is essentially coastal, averaging about 20-30 miles in width. Drainage is by short coastal streams to the sea or into shallow flats and salinas through the porous Plantagenet beds. The vegetation consists of mallee and mallee heath which in the western portion is replaced by stunted jarrah and marri, blackboy (*Xanthorrhea preissii* Endl.), grass tree (*Kingia australis* R. Br.), and *Grevillea* spp. The soils are similar to the Narrikup region in that they are dominated by lateritic gravelly sands which are weakly acid to neutral in reaction. The rainfall for the most part exceeds 20 in.

(9) *Avon.*—The area included in this region is practically identical with the Avon region of Teakle and is constituted by the Avon, Jingalup, and part of the Dumbleyung combinations of Smith. Prescott (1931) classes the soils as "red brown earths" and "residual podsols", the former being considered as a zone between the podzolized soils of the coastal region and the calcareous solonized soils of the more arid interior. They show very little influence of the fossil podzol peneplain. Smith (1952) has pointed out that these soils differ in morphology from the red-brown earths of south-eastern Australia and suggests that they be more aptly referred to as south-western brown soils. A typical profile is described as follows:

0-4 in. Grey-brown sandy loam with humus.
4-10 in. Brown sandy loam.
10-24 in. Red-brown sandy, loamy clay.
24+ in. Red-brown light clay.

Besides the brown soils derived from country rock, soils derived from laterite whether *in situ* or re-sorted are important. The former dominate the pattern in the northern part and the latter in the southern. There are restricted areas of sand plain and in the south-east, brown sandy loams underlain by mottled clay subsoils derived from granite are associated with York gum and jam.

The vegetation throughout the region is savannah woodland, the dominants being York gum and jam with wandoo in the south. The rainfall varies from 17 to 25 in.

(10) *Granite Outcrops.*—Throughout the lower-rainfall region (< 20 in.) of the South-West Province the gently undulating topography is frequently broken by the occurrence of hills or tors of Pre-Cambrian granite rock up to 250 ft high and occupying several acres. These outcrops represent batholiths or monadnocks of the second granitic invasion (Clarke, Prider, and Teichert 1944), and their effect has been to create small localized areas which differ edaphically as a result of recent weathering, and climatically as a result of run-off, from the surrounding country. The soil at the base of the rocks usually has a surface of gritty sand which passes to a sandy loam over loamy clay.

Gardner (1942) notes that granite outcrops and their vicinity have a characteristic flora, frequently containing species which are not found elsewhere. In winter months the ground is often carpeted with bulbous Liliaceae, Orchidaceae, *Drosera*, and *Stylidium*. We have noted that jam is frequently a colonizer of these restricted habitats.

(11) *Mt. Ragged.*—About 100 miles east of Esperance and 40 miles north of Israelite Bay a series of rock outcrops constituting the Russell Range rise abruptly from the very gently undulating plain. Geologically they belong to the whitestone phase of the Pre-Cambrian. The formation lies on the extreme easternmost edge of the South-West Province, where the average annual rainfall is about 12 in. Mt. Ragged (1920 ft) is the highest and largest of the peaks.

Clarke and Phillipps (1953) have reported that physiographic evidence suggests the existence of wave-cut platforms at about the 800-ft level on both Mt. Ragged and other peaks of the Range. These shelves were possibly cut during the period of Miocene submergence (Clarke, Teichert, and McWhae 1948).

(12) *Eremean.*—This region constitutes one of the three climatic-vegetation provinces of Gardner (1942), being approximately separated from the South-West Province by the 10-in. rainfall isohyet.

Gardner (1942) describes the area as being a floristically and ecologically impoverished arid region. The flora is derived from the neighbouring provinces and possesses no distinctive elements of its own. Four major vegetative formations are recognizable, i.e. mulga bush, *Triodia* steppe, desert, and the halophytic formations.

The generally flat or very gently undulating topography is occasionally broken by residual hills or rock outcrops. Prescott (1931) classes the variable soils as desert loams. Rainfall is erratic and unreliable.

Genus KENNEDYA Ventenat

Kennedya Vent. in Jard. Malm. 104, t. 104 (1804).

The genus *Kennedya*, a member of the tribe Phaseoleae of the Leguminosae, was first described by Ventenat (1804) and was named after Lewis Kennedy (1775-1818), nurseryman at Hammersmith near London. The literature suggests that the marked similarity between members of this genus and the related genera of *Hardenbergia* Benth. and *Glycine* L. caused some confusion to the early taxonomists.

Black (1948) uses the characteristics given below to distinguish the three genera. In the experience of the authors these characters are satisfactory although few Glycines have been examined.

Kennedya Vent.—Calyx-teeth about as long as tube, the 2 upper ones united in a 2-toothed lip; petals equal; standard with 2 inflexed auricles and 2 small calli about the claw, the lamina spreading; wings adhering to the incurved obtuse keel; stamens 9 and 1; anthers equal; ovary with several ovules; style slender, beardless, with a terminal stigma; pod linear, with pithy partitions; seeds carunculate.

Hardenbergia Benth.—Differs from *Kennedya* in the calyx-teeth much shorter than the tube, the standard without inflexed auricles or calli, the keel much shorter than the wings, the short thick style, and the smaller flowers which are usually in 2's and 3's along the peduncle.

Glycine Lindl.—Calyx with the 2 upper teeth united to about the middle; standard suborbicular; wings slightly adherent to keel, which is obtuse and shorter than wings; upper stamen usually becoming free; anthers equal; ovary with several ovules; style short, glabrous; pod linear, with pithy partitions between the seeds which are without caruncle.

Species Taxonomy and Distribution

Gardner (1931) lists 11 *Kennedya* species as occurring in Western Australia, all of which except *K. glabrata* (Benth.) Lindl. have been located and collected. In addition there are two species which are entirely confined to eastern Australia, viz. *K. rubicunda* Vent. and *K. retrorsa* Hemsl.

The brief descriptions of each species given below under appropriate headings have been made sufficiently wide to include all recognizable variations. Species are fairly uniformly distinct in floristics but are broken up into varying numbers of biotypes on a basis of variation in certain other characteristics, notably habit, leaf shape and size, departure from the normal trifoliate arrangement of leaflets, the size of flowers, and the nature of the inflorescence.

When morphologically distinguishable variants, each restricted to an ecologically distinct area, maintain their characteristics when grown under uniform conditions, each variant is described as an ecotype.

It should be noted here that evidence of Silsbury (unpublished data) shows that self-fertilization is common if not the rule in *K. prostrata*, *K. carinata*, *K. eximia*, *K. nigricans*, *K. microphylla*, *K. beckxiana*, and *K. stirlingii*.

A new key to the classification of the genus constitutes Appendix I. This follows the same pattern as that given by Bentham (1864), but is extended to include all described species.

Distributions in relation to the regions described above are recorded for each species after the taxonomic descriptions. These are shown in Figures 1-3.

Fig. 3.—Map of the South-West Region of Western Australia, showing distribution limits of *K. eximia* Lindl. (*D*), *K. stirlingii* Lindl. (*E*), *K. nigricans* Lindl. (*F*), *K. microphylla* Meissn. (*G*), *K. glabrata* (Benth.) Lindl. (*H*), *K. macrophylla* (Meissn.) Benth. (*J*), *K. beckxiana* F. Muell. (*K*), and *K. prorepens* F. Muell. (*L*)

1. **K. microphylla** Meissn. in Lehm., Pl. Preiss. **1**: 91 (1844).

Description.—A small prostrate species, with branching runners, sprinkled with a few stiff hairs. Leaflets 3, broadly obcordate, herbaceous, under 0.5 in.; stipules small but broad, striate, deciduous; stipellae absent; bracts small, deciduous. Flowers smallest of genus, brick-red; standard orbicular, 0.3 in. dia.; keel obtuse, as long as wings. Peduncles long, axillary, 1-3 flowered; pedicels short. Pod short, under 0.75 in., glabrous, flat or with convex valves. Seeds very small.

Distribution.—Western part of South Coastal region. Here it shows a preference for only one habitat, namely, the flats dominated by the swamp yate

(*Eucalyptus occidentalis* Endl.), an association found on sandy-surfaced heavy-textured clays in lowlying or wash-accumulating depressions. The soil is subject to waterlogging in winter.

2. **K. stirlingii** Lindl., Bot. Reg. t. 1845 (1837).

Description.—Prostrate or semi-erect, rarely twining, tending to woodiness in older plants. Leaflets 3, obovate, lanceolate, sometimes slightly undulate, 1.0-2.5 in. Stipules large, leafy; stipellae linear; bracts broad, persistent, often 3-lobed; plant hirsute. Flowers slightly larger than *K. carinata*, brick-red; standard orbicular; keel obtuse, slightly shorter than wings. Peduncle 1-3 flowered, equal to or longer than pedicel. Pod turgid with convex valves, coriaceous. Seeds large.

Distribution.—Northern part of the Darling region. The species grows prolifically in the more open areas on slopes of dissected laterite, where young soils are developing on country rock, or the kaolinitic clays of the eastern margin. It is not found on untruncated laterite profiles and appears to be limited eastwards by about the 25-in. isohyet. Northward extension is limited by a regional boundary but no major climatic or edaphic factors can be related to its failure to spread south, where both soil and rainfall appear to be favourable.

3. **K. carinata** (Benth.) Domin, New Add. Fl. W. Aust. (Prague) 41 (1923).

K. parviflora Meissn. in Lehm., Pl. Preiss. **1**: 91 (1844).

Description.—Prostrate or trailing, sparsely but stiffly pubescent. Leaflets 3, obovate or broadly obcordate-truncate, rarely under 0.5 in., normally 0.5-1.0 in. but may reach 1.5 in. Stipules leafy, acute, veined; stipellae linear, acuminate; bracts broad and stipule-like. Flowers smaller than any species except *K. microphylla*, violet; peduncles longer than pedicel, 1-6 flowered, central pedicel sometimes bearing 2 flowers; standard orbicular, 0.6 in. dia.; keel somewhat obtuse, nearly as long as wings. Pod short, about 0.75 in., very turgid, coriaceous, glabrous or pubescent.

Distribution.—South part of Darling region, most of the Chapman and Nornalup regions. Good correlation between the 7-month growing period and the general limits of distribution is evident, particularly in the Darling region. To the south-east this relationship fails, as the soils of the Narrikup and South Coastal regions appear to be unfavourable to the species. Throughout the three regions first mentioned, association with jarrah and marri occurs, particularly vigorous growth being made on soils derived from disturbed laterite horizons such as the Bangalup series (Smith 1951). Over the Chapman region the species is restricted to the shallow depressions with a soil of clayey sand over clay subsoil. Extension into the southern part of the Swan Littoral region occurs south of Busselton, where several vigorous communities are found on the gravelly and alluvial soils over outwash from the low plateau.

4. **K. coccinea** Vent., Jard. Malm. 104, t. 105 (1804).

Description.—Prostrate or twining, robust, often woody. Leaflets coriaceous, harsh, normally 3 but may be 5, 7, or 9 with occurrence of accessories, linear, lanceolate, ovate, orbicular, obcordate, truncate, cuneate, sometimes lobed.

Stipules narrow, deltoid, acuminate with prominent veins; stipellae small, linear. Flowers red; standard orbicular; keel conspicuously shorter than wings. Peduncles long and always vertical; pedicels very short. Flowers 4-20 in umbels or loosely so. Young flower buds and lower leaf surface rust pubescent. Pod compressed, normally only 2-3 from each umbel.

Distribution.—Darling, Chapman, Nornalup, Narrikup, and South Coastal regions. General limits of distribution lie to the inside of the 6-month growing period, the gap being wider in the south-east. The species in the 3 former regions favours the undisturbed laterite soils and is rarely found on soils over country rock. Near Rocky Gully limited development occurs on the lower levels of the Kwilalup association. A large number of leaf variants are encountered on the laterites of the Narrikup region, and it is within this area near Albany that communities showing leaflet number variants (see *Description*) are found.

Distribution becomes more discontinuous eastward over the South Coastal region. In fact beyond the 25-in. isohyet only a few very widely isolated communities are found.

5. **K. eximia** Lindl. in Paxt. Mag. **16**: 35 (1849).

Description.—Prostrate, sometimes twining. Leaflets 3, markedly veined, ovate, obovate, lanceolate. Stipules broad, sometimes leafy, acute, veined, deciduous. Bracts small, deciduous. Plant silky-villous. Flowers scarlet, 1-6 in umbel or short raceme; peduncle longer than pedicel. Standard broadly obovate, sometimes orbicular; keel curved, obtuse; wings fully as long as keel but not as broad. Pod glabrous or slightly pubescent, often curved, narrow and flattened.

Distribution.—South Coastal region, southern part of the Avon region, and south-eastern corner of the Darling region. The species is of limited distribution and shows no observable correlation with any single climatic feature. It is, however, tolerant of low-lying, relatively wet habitats, being confined in the South Coastal region to the poorly drained depressions, edges of yate flats, and slopes of the drainage channels such as the Lort and Oldfield Rivers. Near Esperance, association with clumps of mallee has been noted. Plants constituting an isolated colony in a sand-filled drainage line at the base of Mt. Madden, north of Ravensthorpe, show no divergence from the normal.

The north-east corner of the distribution area extends out of the scrub-covered plains into the edge of the Avon region, where vigorous colonies have been found in depressions of loamy soil with jam vegetation. Collections have also been made from the edge of Lake Matilda and the sandy flats with heath vegetation west of Cranbrook.

6. **K. nigricans** Lindl., Bot. Reg. t. 1715 (1835).

Description.—Robust, woody climber capable of prolific growth, but normally stunted. Leaflets 1-3, ovate, up to 5 in. in length, tough, coriaceous. Stipules small, cuneate, striate; stipellae small, linear. Bracts small. Plant glabrous or slightly pubescent. Flowers black and yellow, in racemes. Standard narrow-obovate, folded back over calyx; keel almost acute, almost as long as standard. Pod linear, flat. Seeds small.

Distribution.—South Coastal region. The distribution of this unique species is restricted to a narrow coastal strip between Cape Riche and Hopetoun. The area has not been investigated very thoroughly and only 6 collections have been made from the following habitats: sand dune with dune vegetation, deep sand with banksia scrub, gravelly loamy sand in depression with mallee, and loamy sand near the mouth of the Eyre River. Most of the colonies have consisted of no more than a few scattered plants showing little vigour. Recently Willis (1953) has recorded 2 new localities for this species, viz. Middle I. and North Twin Peaks I. in the Recherche Archipelago.

From time to time plants have been cultivated in suburban gardens near Perth and the occurrence of a small but vigorous community on sand over coastal limestone near Fremantle is probably a result of such activity. Black (1948) notes that introductions into South Australia have gone wild in the Adelaide Hills.

7. **K. prorepens** F. Muell., Fragm. **8**: 225 (1874).

Description.—Prostrate, slender, sometimes showing woodiness. Leaflets 3, about 1.0-1.5 in., orbicular, obovate, obcordate, coriaceous, veined. Young parts and lower leaf surface rust pubescent. Stipules broad-based, acute; stipellae very small, linear. Bracts small, acuminate. Peduncle very long, always vertical; flowers blue-mauve, racemose or verticillate; pedicels short. Standard orbicular; wings and keel equal. Young pod glabrous, turgid.

Distribution.—Eremean region. Collections of this species made in the North-Eastern Goldfields south of Wiluna indicate that it is of limited occurrence in association with spinifex (*Triodia*) formations which occur intermittently in the mulga (*Acacia aneura* F. Muell.) zone. Spinifex is found only on dunes or flats exhibiting a sandy surface which becomes compacted with admixture of clay at 18-24 in. *K. prorepens* has been located in the shallow water-ways that spill out over the flats from laterite breakaways or low granite outcrops.

Scattered occurrences are known in the arid regions, collections being reported from Sandstone, W.A. (C. A. Gardner), Norseman, W.A. (N. T. Burbidge), north of Meekatharra, W.A. (E. T. Bailey), Lake Eyre, S.A. (Black), and the Simpson Desert (Elder Expedition).

8. **K. beckxiana** F. Muell., Fragm. **11**: 98 (1198) (1880).

Description.—A coarse woody twining plant, reaching up to 6-10 ft in length. Leaflets 3, lanceolate, ovate, 1.5-2.0 in. Stipules small but broad-based; stipellae linear. Bracts of the peduncle very broad and leafy, connate, veined, persistent. Flowers large, 1-5 in loose umbel. Peduncle and pedicel equal in length. Standard narrow-obovate as in *K. prostrata*, red, with yellow patch at base. Pod long, 4-5 in., narrow, entirely glabrous, coriaceous.

Distribution.—Mt. Ragged. This is the only known locality for this species. It is found above the level of the wave-cut platform on shallow sands. Other peaks of the Russell Range to the north-east of Mt. Ragged have not been examined for the occurrence of this species but a few lesser ones to the south-west have failed to reveal any new communities.

9. **K. macrophylla** (Meissn.) Benth., Fl. Austr. **2**: 252 (1864).

Description (from herbarium material).—A tall, coarse, twining species, loosely hirsute with spreading hairs, silky on the young parts. Leaflets 3, obovate or orbicular, very obtuse, often above 2.0 in. long. Stipules very broad, often united and attaining 1.0 in. in diameter; stipellae lanceolate. Flowers red, distinctly racemose on axillary peduncles. Bracts deciduous. Pedicels rather short. Standard orbicular, nearly 0.5 in. in diameter; keel very much curved, obtuse, nearly as long as the wings. Pod glabrous, very turgid, about 1.5 in. long, acuminate with a persistent style.

Distribution.—Specimens from near Augusta are included in the State Herbarium. A collection has recently been made from this locality.

10. **K. glabrata** (Benth.) Lindl., Bot. Reg. t. 1838 (1837).

Description (from herbarium material).—A slender twining species. Leaflets 3, cuneate or obovate, truncate, mucronate, 0.5-1.0 in. long. Stipules leafy, broad, veined. Bracts none or very deciduous. Calyx short, upper lobes forming an obtuse, emarginate lip. Standard orbicular; wings much falcate; keel incurved, almost acute or shortly acuminate. Flowers umbellate. Plant glabrous or with a few spreading hairs. Pod glabrous, very turgid, under 1.0 in. long.

Distribution.—Reported from near Albany and included in the Lindley collection.

11. **K. prostrata** R. Br. in Ait., Hort. Kew, 2nd ed. **4**: 299 (1812).

General Description.—Prostrate or trailing with sometimes branching runners 2-10 ft; hirsute-densely pubescent. Leaflets 3, rarely 1 or 2, ovate, obovate, lanceolate, orbicular; herbaceous, 0.5-3 in. in length, margins crenate, undulate, sometimes entire. Stipules large and leafy; stipellae large and acute; bracts large, cordate, sometimes connate, persistent. Flowers large, normally under 1.0 in., bright scarlet-pink; standard narrow obovate; keel linear, almost acute; wings usually slightly shorter than keel, linear. Peduncle short, 1-6 flowered; pedicels long, the central one sometimes bearing 2 flowers. Pod cylindrical, coriaceous, glabrous or pubescent. Seeds large.

Description and Distribution of Ecotypes.—*K. prostrata* shows a much greater range of variability than any other species, particularly in habit and leaf size. In several instances such variation is distinctive and localized, and since transplantations have shown that distinguishing characteristics have a genetic basis, these populations are described as ecotypes, a key to which constitutes Appendix II (see also Fig. 4).

(i) *North coastal.*—Leaflets large (2.0-3.0 in.), herbaceous, ovate-obovate, margins entire or slightly undulate. Bracts large, connate. Plant almost glabrous with few appressed hairs. Pod glabrous. Stems thick and fleshy. Spreading to 6 ft. *Distribution.*—North Coastal region.

(ii) *West coastal.*—Leaflets medium (1.5-2.0 in.), herbaceous but becoming coriaceous at maturity, ovate; margins undulate. Bracts large and leafy, sometimes connate. Plant densely pubescent, young parts silky-villous. Stems thick, becoming woody. Pod pubescent. Spreading to 8 ft. *Distribution.*—Northern part of Swan Littoral region, on alluvium, sands, and stable dunes.

(iii) *Savannah.*—Leaflets medium (1.0-2.0 in.), herbaceous, ovate-obovate, lanceolate; margins crenate. Bracts smaller than (ii), sometimes connate. Plant slightly and finely pubescent. Stems thick and fleshy. Pod glabrous. Spreading densely and vigorously to 10 ft. *Distribution.*—This type represents the species in its most vigorous and prolific form in the region of savannah woodland on the south-western brown soils of the Avon region and related soils of the North Sub-coastal region. It has been found to show consistent association with York gum and jam, particularly on the eastern edge of the region.

Fig. 4.—Map of the South-West Region of Western Australia, showing distribution of ecotypes of *K. prostrata* R. Br.

(iv) *Forest.*—Leaflets small (under 1.0 in.), herbaceous, usually orbicular but sometimes ovate; margins crenate. Bracts small. Plant slightly but stiffly pubescent. Stems slender, rarely woody. Pod glabrous. Straggling or sparsely spreading to 4 ft. *Distribution.*—Darling, Chapman, Nornalup, and Narrikup regions, where it is found on sandy-surfaced soils of either undissected or re-sorted laterite, and southern part of the Swan Littoral region on alluvium.

(v) *South coastal.*—Leaflets small (under 1.0 in.), herbaceous, thick obovate-ovate; margins markedly crenate. Bracts small but leafy. Plant densely pubescent. Stems thicker than (iv) and fleshy. Pod pubescent. Spreading sparsely to 2-3 ft.

Distribution.—Eastern part of the South Coastal region, where it behaves ecologically like *K. eximia* in that it is restricted to depressions and drainage channels.

(vi) *Inland.*—The form associated with the granite rocks (region 10) appears to be a smaller (leaflets 1.0-1.5 in.) and less vigorous variant of the savannah type. It is separated from it, however, on the basis of its distinctive distribution pattern and ecology.

Present Trends in Distribution

A feature of the ecology of *K. prostrata*, *K. coccinea*, and *K. carinata*, and to a lesser extent *K. prorepens*, is the frequency of occurrence of prolific growth on disturbed habitats, particularly following clearing and/or burning of the vegetation. These dense stands do not persist for more than 2 or 3 years as the plants usually succumb to competition and grazing. A high proportion (about 80 per cent.) of the seeds of these species are known to be "hard", and it is from this source that new colonies arise when conditions favourable to germination and establishment occur. Capacity to produce impermeable (hard) seeds could well be selected for in natural populations since it confers the advantage of lack of response to unseasonal rainfall. Hard seeds represent a germination potential which can be released at slow and regular intervals over periods of several years.

The capacity for response to disturbance exhibited by the above four species appears to have resulted in an increase in the number and size of communities in areas where land is in process of preparation for agricultural or pastoral production. Such increase, however, is only temporary owing to non-persistence, so that the net effect of complete conversion to cropping or grazing has been a decrease in numbers. In such cases the only habitats left for colonization are roadsides and small pockets of uncleared or protected land.

Discussion

In considering the origins of the elements which go to make up the Western Australian flora, Gardner (1942) states that "there are several groups which, while perhaps of palaeotropic origin, have become so modified or have undergone such an extensive development that they are no longer recognisable as typical examples. Indeed, in some cases they have assumed such importance in Australia that they have been regarded by some authors as typifying the Australian Element". The order Leguminosae is considered as an example.

The genus *Kennedya*, in view of its close relationship to the Glycines, and the fact that the Phaseoleae are not richly developed in Australia, is undoubtedly of Indo-Melanesian origin. Crocker and Wood (1947) have suggested that an invasion of Australia by this element occurred during Miocene times in response to warmer conditions. Whilst *Kennedya* species cannot be considered as typical of the Australian Element, the fact remains that they are endemic to this continent and show a considerable degree of adaptation to existing climatic and edaphic conditions.

Three factors appear to have been important in determining the present pattern of variability and distribution:

(i) The common occurrence of self-fertilization;
(ii) Tertiary and post-Tertiary climatic changes;
(iii) The present pattern of climate and soils.

The adoption of an inbreeding system by a species is considered by Darlington and Mather (1949) to influence its evolutionary history. A normally inbred species is expected on theoretical grounds to exhibit a high degree of immediate fitness to its environment. Such fitness, however, can only be achieved at the expense of flexibility, i.e. of ability to adapt to changing conditions. Inbreeding systems, then, represent evolutionary "blind alleys", and species with this method of reproduction will ultimately be eliminated in a changing environment. A degree of environmental stability appears to be a prerequisite for the maintenance of inbreeding groups, a relationship evidenced by the genus *Kennedya* in the south-west of Western Australia.

It is now also considered (Darlington and Mather 1949; Stebbins 1950; Baker 1951) that the pattern of distribution of self-fertilized species tends to be that of a number of at least physiologically distinct biotypes, each of which is more or less adapted to a particular environment or aspect of an environment. *K. prostrata*, the most widely distributed species, tends to follow this pattern in that it shows the development of a number of distinguishable variants, the limits of which can be defined on a regional basis. The "leaflet shape" and "leaflet number" variants of *K. coccinea* also show some degree of localization but the pattern is not referable to environmental divergence as with *K. prostrata*.

Crocker and Wood (1947) have considered the development of the Australian flora in relation to palaeoclimatological and palaeopedological processes. They present evidence in favour of the separation of an early pan-Australian flora by the Miocene seas, with the consequent floristic isolation of the south-west of the continent, and suggest that this isolation has been maintained more or less continuously since the Pliocene by climatic and edaphic barriers. The south-west is not held by these authors to be the centre of origin of the Australian Element, but they consider it "logical to believe that it has been a centre of dispersal at various times". Gardner (1942) notes that the above region is particularly rich in endemic species.

If we consider that progenitors of the present species were established in the south-west prior to or during the Miocene, then the Miocene and post-Miocene climatic and edaphic changes postulated by Crocker and Wood and others have influenced subsequent speciation and distribution. The similarity of *K. rubicunda* to the apparently relict species of *K. nigricans* and *K. beckxiana* suggests that these species are more closely related to the early types which possibly had a pan-Australian distribution. Also it is not unlikely that *K. beckxiana* or its parental types were isolated on Mt. Ragged by the Miocene incursion.

There are several facts which do not support the idea that a division of the distribution of *K. prostrata* occurred at this time. They are:

(i) The lack of any marked divergence between representatives of the species in east and west;

(ii) The continuation of the species in South Australia on the eastern side of the Nullarbor Plain when the climate becomes favourable;

(iii) The more prolific development evident in Western Australia.

It seems logical to conclude then that *K. prostrata* is one of the species that has escaped from Western Australia over the normally isolating barriers, possibly during the pluvial Pleistocene.

The effect on the flora of a post-Miocene period of aridity, for which a Recent age is given by Crocker and Wood (1947) and Browne (1945), was according to the former authors largely threefold. In the first place, there was a general southward contraction of the flora. Secondly, isolated refugia were created into which those elements of the flora withdrew which were able to survive the relatively sudden onset of unfavourable conditions. Thirdly, wholesale destruction of many groups occurred.

Evidence in favour of a southward withdrawal of species is obtained from the facts that nine of the 11 species of *Kennedya* occur along the south coast and that two of these, *K. glabrata* and *K. macrophylla*, are almost extinct and two (*K. nigricans* and *K. beckxiana*) apparently relict. Also the association of small populations of *K. prostrata* and other species with the granite rocks suggests that these localities then, as now, functioned as centres of survival. The pre-arid distribution of *K. prostrata* must have been wider than at present, since the spread of propagules to these outlying habitats is unlikely to have been achieved by biotic or other agencies.

The possibilities that the southern species at present showing limited distributions are of recent hybrid origin is unlikely in view of two lines of evidence of Silsbury (unpublished data). Firstly, the chromosome number of all species is constant and the morphology similar. Secondly, artificial inter-species crosses have failed to produce hybrid progeny. Also species are quite distinct and there is a lack of putative parents.

The account of species distributions in relation to soils and climate given above and summarized in Figures 1-4 indicates that those species which are not limited to restricted habitats show a fairly immediate relationship to these factors. The successive approximate restriction of *K. carinata*, *K. coccinea*, and *K. prostrata* by the 7-, 6-, and 5-month growing periods respectively, as we progress from the high-rainfall areas of the extreme south-west into those of lower rainfall, shows an increasing degree of species adaptation to increasing aridity. These species were apparently able to colonize the new habitats created by the recession of arid conditions much better than any others. Their still evident ability to rapidly colonize disturbed habitats is most likely one reason for their success.

Soils supporting *Kennedya* species are, excluding the south-western brown soils and the desert loams, predominantly podzolic or lateritic in nature and aré known to be inherently low in fertility (Smith 1952). Differences in actual nutrient supply cannot then be considered as materially influencing distribution. A possible exception is the apparent response of the savannah ecotype of *K. prostrata* to the more fertile south-western brown soils. It appears then that the influence of soil on *Kennedya* distribution is through plant : soil : water relations, i.e. that the soil has an effect in controlling the length of the growing period. Such an effect is not revealed by any general consideration of P/E_w values.

The importance of a change in soil type is shown in the south-east of the region, where the incidence of lateritic sand plain restricts the distribution of *K. prostrata* and *K. coccinea* to the more climatically favourable coastal region and eliminates *K. carinata* entirely. The latter species up to this point shows very good correlation with the 7-month growing period. It should be noted that deficiencies of the minor elements copper and zinc, which up to the present time have limited agricultural utilization of the South Coastal region, cannot be a factor in distribution as these deficiencies occur over the whole area.

The South Coastal region, however, provides most of the habitats for *K. eximia* and all habitats for *K. microphylla*. Smith (1952) and Pym (personal communication) consider that conditions similar to those in the habitats of these two species favour the development of laterites under the present climatic cycle. In fact it is not unlikely that climatically and edaphically this area presents conditions similar to those that must have been operative over a wider area during the period of maximum laterization, and that it is for this reason that *K. eximia* and *K. microphylla* have been able to survive.

K. prorepens and *K. stirlingii* do not appear to have reacted to the postulated climatic changes similarly to the other species of the genus. *K. prorepens* flowers prolifically but is known to be unable to set seed under south coastal conditions. This fact may account for its almost complete absence from the South-West Province. The fact that *K. stirlingii* has not completely filled all available habitats suggests that it is a relatively young species and that its distribution area should be increasing. On the other hand, however, the uniformity of the species and its ecological specificity give the impression of an old species at present only surviving in habitats of restricted occurrence.

Acknowledgments

Grateful acknowledgment is made to the Rural Credits Development Fund of the Commonwealth Bank for generous financial assistance to one of us (J. H. S.), to Mr. A. J. Millington for assistance throughout, and to Professor E. J. Underwood, under whose general direction the work has been conducted. We are indebted to Mr. C. A. Gardner and Mr. R. D. Royce for initial information on species localities and for species identification in the early stages.

To our many colleagues and friends who have assisted with collections we owe special thanks.

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Appendix I

KEY TO SPECIES OF THE GENUS KENNEDYA (after Bentham)

A. Standard narrow-obovate; pod compressed; flowers purplish black in a one-sided raceme; woody climber .. .. 1. *K. nigricans* Lindl.

A. Standard broadly obovate, almost orbicular
- B. Woody climbers
  - C. Pod turgid; bracts connate, conspicuous; plant glabrous .. 2. *K. beckxiana* F. Muell.
  - C. Pod compressed; bracts deltoid, acuminate; plant pubescent .. 3. *K. rubicunda* Vent.
- B. Prostrate or rarely twining; leaves usually herbaceous
  - C. Pod turgid; peduncle and pedicel almost equal; bracts large, persistent; stipellae prominent .. .. 4. *K. prostrata* R. Br.

C. Pod compressed; peduncle longer than pedicel; bracts small, deciduous; stipellae inconspicuous; leaflets veined with shining upper surface .. .. .. 5. *K. eximia* Lindl.
A. Standard orbicular or broader than long
B. Peduncle distinctly longer than pedicel and several times longer than petiole; flowers often almost sessile, distinctly umbellate or racemose
C. Flowers loosely umbellate or very shortly racemose
D. Keel conspicuously shorter than wings; leaves coriaceous, harsh . . 6. *K. coccinea* Vent.
E. Pod turgid; leaves about 0.5 in.; 2-many flowered .. 7. *K. glabrata* (Benth.) Lindl.
E. Pod compressed; leaves under 0.5 in.; 1-4 flowered; stipellae absent .. .. 8. *K. microphylla* Meissn.
C. Flowers distinctly racemose
D. Woody climber; bracts large, deciduous; stipules large
E. Pod turgid, glabrous .. .. 9. *K. macrophylla* (Meissn.) Benth.
E. Pod compressed, clothed with reversed hairs .. .. 10. *K. retrorsa* Hemsl.
D. Slender prostrate plant; bracts small, persistent; stipules small; flowers blue-violet .. .. 11. *K. prorepens* F. Muell.
B. Peduncle and pedicel nearly equal in length; peduncle shorter than or equal to petiole; flowers umbellate
C. Peduncles 1-8 flowered; plant prostrate, stiffly pubescent; flowers rose-violet; stipules small; pod 1 in., pubescent .. .. 12. *K. carinata* (Benth.) Domin
C. Peduncles 1-5 flowered, normally 3; plant prostrate-semi-erect, hirsute; flowers brick-red; stipules large and leafy; pod glabrous .. .. 13. *K. stirlingii* Lindl.

Appendix II

KEY TO ECOTYPES OF KENNEDYA PROSTRATA R. BR.

A. Plant almost glabrous or with few stiff or appressed hairs
B. Mature leaflets large, 2.0-3.0 in., margins slightly undulate; plant densely spreading .. .. 1. North coastal
B. Mature leaflets small, under 1.0 in., margins crenate; plant straggling or sparsely spreading .. .. 2. Forest
A. Plant slightly and stiffly pubescent; mature leaflets 0.5-1.5 in.; plant straggling .. .. 3. Inland-Savannah
A. Plant densely pubescent
B. Mature leaflets large, 1.0-2.0 in.; plant large, 6-8 ft, spreading .. 4. West coastal
B. Mature leaflets small, under 1.0 in.; plant small, 2-3 ft, compact .. 5. South coastal

Explanation of Plates 1-7

Photographs of herbarium specimens of *Kennedya* species.

Plate 1

Fig. 1.—*K. prorepens* F. Muell.
Fig. 2.—*K. coccinea* Vent.

Plate 2

Fig. 1.—*K. beckxiana* F. Muell.
Fig. 2.—*K. nigricans* Lindl.

Plate 3

Fig. 1.—*K. stirlingii* Lindl.
Fig. 2.—*K. carinata* (Benth.) Domin.

Plate 4

Fig. 1.—*K. eximia* Lindl.
Fig. 2.—*K. microphylla* Meissn.

PLATE 5

Fig. 1.—*K. prostrata* R. Br. Ecotype, north coastal.
Fig. 2.—*K. prostrata* R. Br. Ecotype, west coastal.

PLATE 6

Fig. 1.—*K. prostrata* R. Br. Ecotype, forest.
Fig. 2.—*K. prostrata* R. Br. Ecotype, savannah.

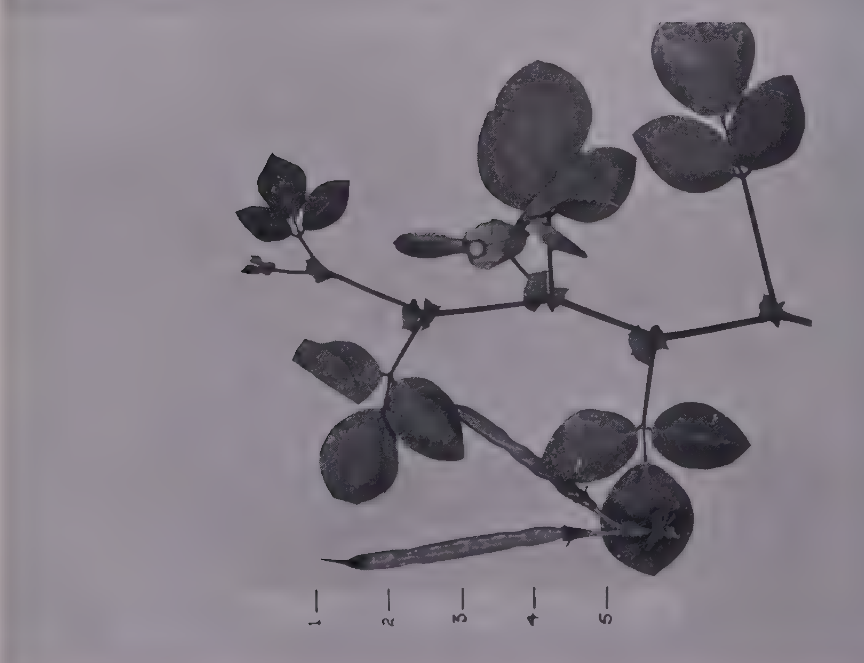
PLATE 7

K. prostrata R. Br. Ecotype, south coastal.

GENUS KENNEDYA IN WESTERN AUSTRALIA

GENUS KENNEDYA IN WESTERN AUSTRALIA

2



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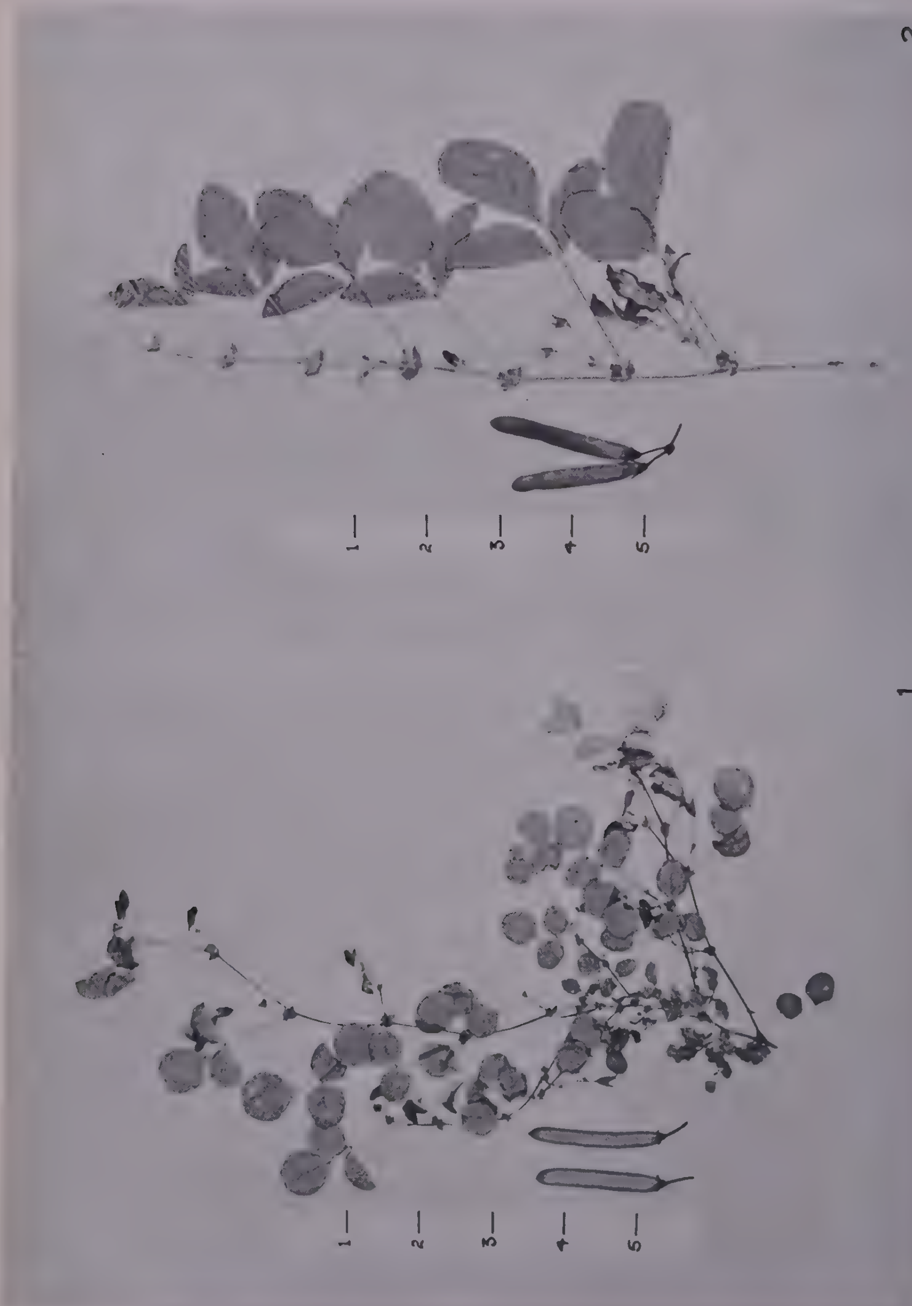

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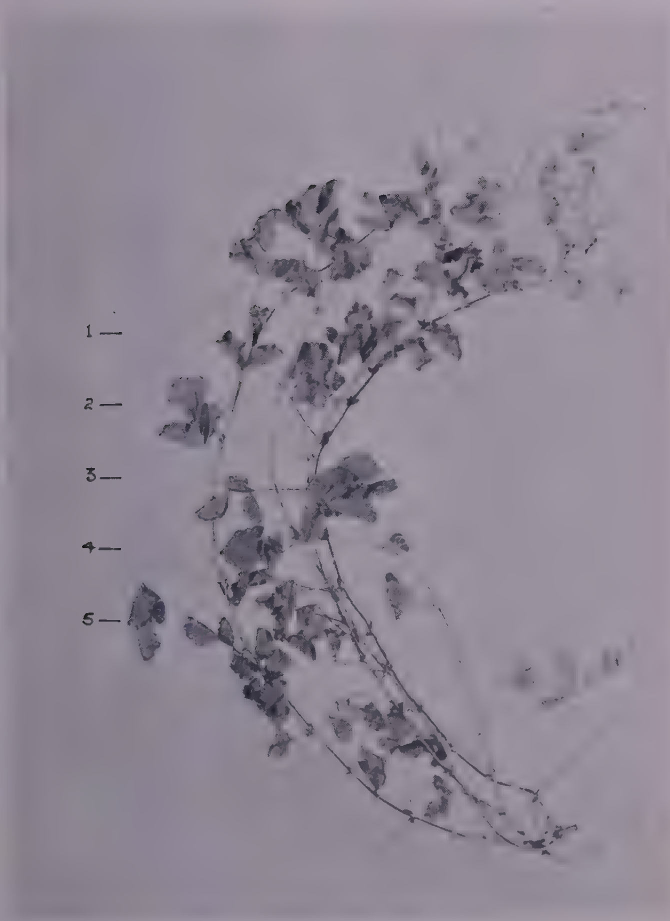

CONTENTS

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THE MECHANISM OF SURFACE GROWTH IN PARENCHYMA OF *AVENA* COLEOPTILES

By A. B. Wardrop*

[*Manuscript received March* 8, 1955]

Summary

A study has been made of the organization of the cell wall in the parenchyma of *Avena* coleoptiles at successive stages of growth, using light and electron microscopic methods. It has been observed that extension of the parenchyma involves a progressive separation of the primary pit fields accompanied by an increasing dispersion of the cellulose microfibrils about their preferred direction of orientation. On the basis of this, and ancillary evidence from other cell types, it is suggested that extension growth involves stretching of the cell with the intercalation of new microfibrils into the expanding cell wall framework from the regions of the primary pit fields and penetration of the cell wall by plasmodesmata. It is considered that the evidence is consistent equally with the view either that the cell wall is stretched as water absorption accompanying enlargement takes place, or that cell enlargement is controlled by the synthesis of cell wall material at synthetic centres (pit fields and plasmodesmata) distributed over the cell surface. The concept of bipolar tip growth for coleoptile parenchyma is rejected.

I. Introduction

The formulation of possible mechanisms involved in the surface enlargement of plant cells has involved extensive study of changes in the cell wall organization and of cell physiology during growth (see Heyn 1940; Audas 1949). A satisfactory synthesis of the evidence from these two lines of investigation cannot be said to have been achieved although such a synthesis is fundamental to our understanding of the growth process.

Of basic importance in any such problem is the question of the mechanism of auxin action in cell extension, and this paper is presented as a step in an attempt to throw further light on this problem.

Following the many proposed mechanisms of extension growth in coleoptile parenchyma reviewed by Heyn (1940), the main electron microscopic study has been carried out by Mühlethaler (1950). From this work it was concluded that extension growth of the parenchyma took place by a polar or biploar tip growth. He found that at an early stage the parenchyma showed corner thickenings composed of longitudinally oriented microfibrils similar to those apparent in Plate 1, Figure 1, which were considered to preclude further extension in those regions of the wall between the thickenings, and that in some cells the walls were noticeably thinner and looser in texture towards their ends, which was regarded as indicating that active terminal deposition of microfibrils took place. It was thus proposed by Mühlethaler that extension took place by an extension of the protoplast through the structurally attenuated tips of the parenchyma, enabling penetration between

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adjacent cells, and that new cell wall material was deposited behind the advancing protoplast. Such a mechanism has also been shown to operate in the extending fibres and tracheids during differentiation (Wardrop 1954).

For cells in which growth is not polar, different mechanisms have been proposed (Stecher 1952; Wardrop 1954). According to Frey-Wyssling and Stecher (1951) and Stecher (1952), in this case the cell wall is penetrated by the protoplast at points on its surface. Here localized cytoplasmic synthesis takes place, locally displacing the microfibrils and enlarging the surface. Into these enlarged "thin areas" are subsequently woven new microfibrils, ultimately closing the enlarged area. An alternative view to this "mosaic growth" of Frey-Wyssling and Stecher was proposed by the writer (Wardrop 1954). On this view growth proceeds not at points of transient protoplasmic penetration of the wall but in the more permanent regions where plasmodesmata penetrate the wall either singly or in aggregates (primary pit fields). Evidence was presented to suggest also that these regions are active in cellulose synthesis, and in terms of such a hypothesis certain features of the minute anatomy of the cell wall can be explained.

If the above mechanisms be considered in relation to the problem of auxin activity in controlling cell elongation, it may be recalled that auxin has been proposed as acting either directly on the cell wall colloids producing a change in plasticity of the cell wall, on the protoplast, or on the uptake of water by the cell (for review see Audas (1949)).

Considering these possibilities in relation to the above mechanisms it is not clear that the morphological studies give any definite support to any of these viewpoints. Nor is earlier morphological literature unequivocal on this point. Thus Bonner (1935) observed in coleoptile parenchyma that the sign of birefringence did not change during elongation, whereas using a different technique Preston (1938) did observe a change in the major extinction position from transverse to an inclined position in coleoptiles at different degrees of elongation, and a similar observation was made for the staminal filaments of certain grasses by Frey-Wyssling and Schoch-Bodmer (1938). Clearly, if there is a change in orientation of the cellulose microfibrils during elongation, then this is consistent with the concept of mechanical stretching of wall. If no such change in orientation takes place then growth cannot be simple stretching and presumably there is some auxin-induced change in the texture of the cell wall which operates over the entire cell surface.

These considerations point to the desirability of some further study of the cell wall texture and organization during extension growth. As a preliminary step, the observations presented here are aimed at elucidating the structural changes in coleoptile parenchyma during normal growth under the correlative control of endogenous auxin. In a further study it is intended to examine similar changes in excised segments *in vitro*.

II. Experiments and Results

The main experimental material used in the present study was the coleoptiles of *Avena sativa* L. (var. Algeribee). The husks were removed and the seeds soaked

in water for 4 hr in darkness, exposed to light with the groove of the seed downwards in a petri dish on damp filter paper for 16 hr, and then planted in moist sand. The coleoptiles were harvested at various stages (see below) for examination.

The investigations of Tetley and Priestley (1927) have shown that the growth in *Avena* coleoptiles proceeds for the most part by simple elongation of the parenchyma. It was shown further by Avery and Burkholder (1936) that cell division is complete by the time the coleoptile is approximately 1 cm in length and that during elongation subsequent to this stage the zone of growth gradually shifts from the

TABLE 1

THE NUMBER OF PIT FIELDS PER CELL AND DIMENSIONS OF PARENCHYMA FROM AVENA COLEOPTILES AT DIFFERENT STAGES OF EXTENSION

Stage of Growth of Coleoptiles		Average Parenchyma Length*	Average Parenchyma Breadth	Average No. of Primary Pit Fields per Cell	Average No. of Primary Pit Fields per 1000 μ^2 of Cell Surface
Stage	Length (mm)	(μ)	(μ)		
1	9·4	141	52	104	147
2	20·2	191	67	102	94
3	25·0	251	68	74	39
4	34·0	238	72	84	51
5	52·0	422	86	97	35

* Average of 50 measurements.

base towards the tip. There is no cell enlargement between the pore and the apex of the coleoptile. Thus in the present study the terminal 3 mm was discarded and the adjacent 5 mm used for examination. Maceration of the coleoptiles was effected by alternate extractions with 1 N sodium hydroxide and by 1 N hydrochloric acid and the macerated material finally washed in distilled water.

Optical examination of the macerated parenchyma was carried out after staining with congo red (0·1 per cent. in dilute sodium hydroxide) using a green filter. For electron microscopic examination the parenchyma was mounted on collodion-covered grids and shadowed with uranium at an angle of 8°. An R.C.A. type E.M.T. electron microscope was used with an initial magnification of 3000. Electron micrographs so obtained are shown in Plates 2-5.

The coleoptiles were harvested at stages shown in Table 1. The average length and breadth of the parenchyma were determined and are also recorded in Table 1, and detailed values are plotted in Figure 1. For reasons described in Section III, it was necessary to determine the number of primary pit fields in parenchyma from

coleoptiles at each stage. This was done by preparing photographs similar to those in Plate 1, Figures 2 and 3, and counting the primary pit fields. Average numbers at each stage of extension are listed in Table 1 and the number per cell is plotted against length in Figure 2. Statistical analysis of these results showed that the number of primary pit fields per cell does not change in cells of increasing length.

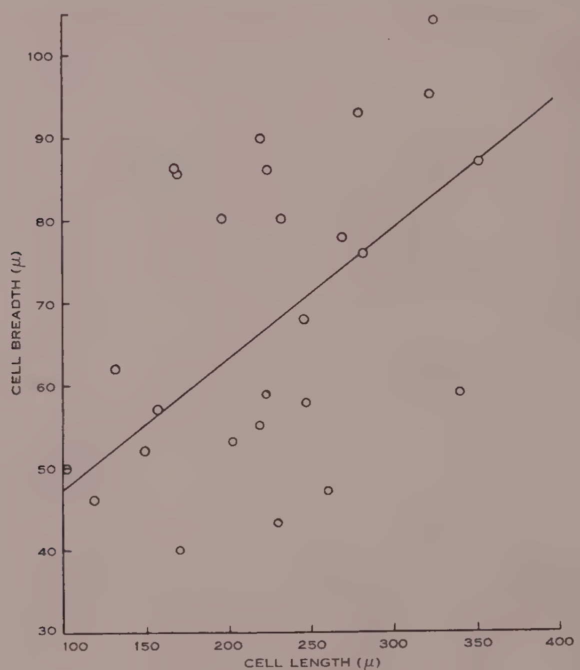

Fig. 1.—Parenchyma cell dimensions (see text).
Breadth = 0·156 length + 32.
(r = 0·59, significant at 1 per cent. level.)

For reasons which will become apparent in the following discussion it was found necessary to examine material other than coleoptiles to supplement some of the arguments advanced. For this purpose parenchyma was examined from the extending root of *Vicia faba* L. and of *Pisum sativum* L., the peduncle of *Narcissus* sp., and the cortex of apple (Granny Smith). The techniques employed were identical with those for coleoptiles, and electron micrographs of this material are shown in Plates 5-8.

III. Discussion

Examination of parenchyma taken from coleoptiles near the beginning and end of the phase of extension growth (stages 1 and 5, Table 1) shows considerable differences. Thus, comparing the photomicrographs (Plate 1, Figs. 2 and 3) it can be seen that early in the extension phase the primary pit fields are greatly crowded (Plate 1, Fig. 2), whereas towards the end of the extension phase the pit fields are

widely separated and less extended in the tangential direction (Plate 1, Fig. 3). In the longitudinal direction the bands of secondary thickening described by Mühlethaler (1950) can be seen (Plate 1, Figs. 1 and 2). From Table 1 and the statistical analysis (see also Fig. 2), it can be seen that the number of primary pit fields per cell does not change in parenchyma from coleoptiles at different degrees of extension. From Plate 1, Figures 2 and 3, and Table 1, it is apparent that the number of pit fields per unit area of the cell surface decreased in cells of increasing length.

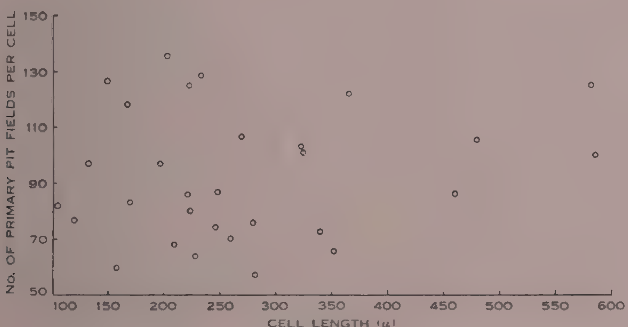

Fig. 2.—Primary pit fields in parenchyma cells (see text).

These observations raise the question of how this separation of the primary pit fields is achieved and of its significance in the surface growth of the cell wall. If, as seems reasonable, it is assumed that the primary pit fields are not transient structures in the sense of being dissolved and re-created, then, because of the different appearance of the cells, the conclusion that growth must have taken place over the entire surface of the cells seems inescapable.

Such a view appears possible in terms of the idea (Wardrop 1954) that the pit fields and points of penetration of the wall by plasmodesmata are centres of cellulosic and of protoplasmic synthesis. Thus, if these are regarded as sources of new microfibrils, then the question arises as to what happens to the cell wall in the regions between the pit fields. For this purpose electron microscopic examination of parenchyma from coleoptiles at different stages of extension was undertaken. Parenchyma cell wall from stage 1 (Table 1) is shown in Plates 2 and 3, from stage 4 in Plate 4, and from stage 5 in Plate 5, Figure 1. In Plates 2 and 3, the microfibrils are densely packed and oriented almost transversely to the longitudinal cell axis. In Plate 3, Figure 2, a large number of primary pit fields is shown. In Plate 4 (stage 4), the microfibrils are noticeably less well oriented with respect to each other, and this becomes even more obvious in Plate 5, Figure 1 (stage 5).

This change in cell wall texture associated with the wider separation of the pit fields in the extended cells suggests that the increase in surface area of the cells has involved at least some stretching of the regions between the pit fields of the cell wall.

Supplementary evidence of this can be found in the extending roots of *Vicia* and *Pisum*. Plate 6, Figure 1, shows the cell wall of parenchyma at or immediately behind the tip in *Vicia*, whereas Plate 6, Figure 2, was from an intermediate position, and Plate 7, Figure 1, was taken from the zone in which extension had ceased. In Plate 7, Figure 2, mature parenchyma of *Pisum* is shown. These micrographs may be compared with those of the later stages of extension in the *Avena* coleoptile (Plates 4 and 5). It is of interest to compare the cell wall texture of, say, Plate 6, Figure 2, and Plate 7, Figure 1, with Plate 5, Figure 2, which is a protoxylem element from the zone 5-8 mm from the root tip of *Pisum*, and represents a type of cell extended by mechanical stretching of the tissue. The similarity between these photographs at the least is not contradictory to the idea that the texture change of the wall during extension involves some stretching of the cell wall.

The above evidence to this stage appears consistent with the view that growth in the coleoptile is accompanied by stretching of the cell wall, it being assumed on the hypothesis previously advanced that the primary pit fields act as centres for the synthesis of new microfibrils.

A further feature of interest is that the elliptically shaped primary pit fields of coleoptile parenchyma are elongated transverse to the cell axis. In the more mature parenchyma they become broader compared with their length (Plate 1, Fig. 3). It is not clear whether this results from secondary thickening of the wall or whether the change in orientation of the microfibrils of the primary wall associated with cell elongation is involved. The changed orientation of the microfibrils seen in Plate 4, Figures 1 and 2, suggests the latter possibility (cf. Plate 2). It may be noted that the transversely elongated elliptical pit fields are also present in other elongated parenchyma such as that from the peduncle of *Narcissus* (Plate 1, Fig. 5). On the other hand, in more or less isodiametric parenchyma as that from potato tubers (Wardrop 1954) and from the cortex of apples (Plate 8, Fig. 1) the pit fields are more nearly circular.

It may be noted further that a change in form of the cell results in a change in the distribution of stress in the wall of the developing cell. Thus, both van Iterson (1936) and Castle (1937) have pointed out that in a cylindrical cell the tangential stress in the wall is twice the longitudinal stress, whereas in a spherical cell the stress on the wall would be the same in all directions at all points. While it is not suggested that the stress alone can govern the orientation of the microfibrils or of the pit fields, it is possible that the orientation is a result of the localized strains (growth) in the wall at any point. The comparison of the foliate texture (Frey-Wyssling 1936) of isodiametric parenchyma of apples and potatoes with the elongated parenchyma of *Avena* and *Narcissus* is suggestive in this regard.

To recapitulate: on the evidence presented, it is suggested that extension growth in the parenchyma of the *Avena* coleoptile may take place, primarily by stretching growth with the intercalation of new microfibrils into the expanding cell wall from the primary pit fields. Since growth takes place under conditions of turgor, stresses operative in the wall may govern the orientation of the microfibrils. This is reflected in the shape of the primary pit fields.

Two consequences of the above study must now be considered; first, the relation of the above results to those of other workers, notably Mühlethaler (1950) and Stecher (1952); and, secondly, what implications the results may have in relation to the various proposals which have been made concerning the mechanism of auxin action.

The chief structural evidence previously advanced for the view that growth of cell does not involve stretching was the observation that the sign of birefringence of the cell wall of parenchyma was negative, irrespective of the degree of extension of the wall (Bonner 1935), whereas relatively slight extension of the wall by mechanical stretching changed the sign of birefringence of the wall from negative to positive. Preston (1938) objected to the work of Bonner (1935) on the ground that single cell walls were not examined and, when this was done, he did observe a change in the major extinction position during extension of the coleoptile parenchyma. The observations of Preston are, however, open to doubt, as he did not take into account the effect of secondary thickening as subsequently described by Wuhrmann-Meyer and Wuhrmann-Meyer (1939). Thus, the optical data referring to coleoptile parenchyma during extension is in fact inconclusive, and therefore does not present any inconsistency with the present suggestion, supported by electron micrographs such as those in this paper, that in fact some change in orientation of the microfibrils does take place during growth. An example in which the birefringence is known to change with extension, although remaining negative, is seen in the case described by Frey-Wyssling and Schoch-Bodmer (1938) in their work on the extension of the staminal filaments of rye.

Considering the results presented above in relation to the work of Mühlethaler (1950), it should be noted that, as he points out, cells exhibiting rounded ends with attenuated wall texture are not frequently seen. This infrequency may be, as he claims, because wall formation is rapid and so only a few cells show stages of wall formation at any time. On the other hand, it may be that the cells observed by Mühlethaler do not represent the general type of extension for the tissue. In the present investigation it has been observed that cells with the pointed end usually are present on the end of a longitudinal file, the remainder of the cells in the file having truncated ends (Plate 1, Fig. 4), so that it must be assumed, in terms of the concept of tip growth, that even longitudinally adjacent cells do not extend simultaneously. It must also be explained, in terms of polar and bipolar tip growth, how the primary pit fields become separated during extension (Plate 1, Figs. 2 and 3; Table 1), since the number of primary pit fields per cell does not tend to increase with extension and the number per unit area decreases. If new length is added then it must be assumed first that some of the pit fields in a cell such as that in Plate 1, Figure 2 (cf. text Fig. 3(a)) must be eliminated (e.g. by secondary thickening) and new ones must be created in the newly formed parts of the wall added at the ends of the cells (Fig. 3(b)). On general grounds this would not appear probable, especially as there is no evidence in cells, such as that shown in Figure 3 of Plate 1, in which considerable extension had taken place, of the elimination of primary pit fields.

On the other hand, if stretching growth does take place, it is necessary to consider how this could be possible when already some longitudinally oriented

bands of secondary thickening were present in cells relatively unextended (Plate 1, Figs. 1 and 2). It is usually assumed that a longitudinally oriented cellulose system is incompatible with stretching. This assumption is probably made by analogy with the very slight elastic extension which takes place on stressing mature fibres with almost axial orientation, such as ramie and flax. It must be emphasized that this observation refers to mature and usually dry fibres. However, there is some evidence that in growing cells this condition does not necessarily hold. Thus the cells of collenchyma, which are capable of considerable extension growth, possess

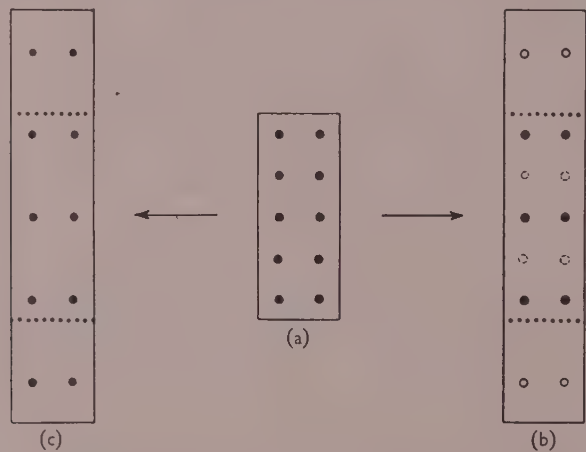

Fig. 3.—A diagrammatic representation of alternative possibilities to explain the observed increasing separation of primary pit fields (black) with a change in cell length. (*a*) Cell before extension; (*b*) as extended by bipolar tip growth with the creation of new pit fields (circles) and the closing of some of the original ones (broken circles); (*c*) as extended by simple stretching.

an almost axial orientation of the microfibrils (Majumdar and Preston 1941) and an unequal thickening of the cell walls. Some of the walls never thicken from the primary condition and can be regarded in this sense as broadly analagous to the condition in *Avena* parenchyma. However, it is not clear what the mechanism of extension in collenchyma is. Like *Avena* parenchyma, these cell walls are high in pectin content, to which Majumdar and Preston (1941) attribute their great extensibility. If such extension occurs, then this would be expected to involve movement between adjacent microfibrils parallel to their length. Such a relative flow between adjacent microfibrils would appear quite feasible since in the fresh cell wall the microfibrils are widely separated by non-cellulosic constituents (hemicellulose, pectins, etc.).

Thus, it would appear that the existence of longitudinal bands of secondary thickening in the cell walls of parenchyma does not constitute an insuperable obstacle to the concept of an overall stretching of the cell wall. Taking into account

the above evidence of the increasing separation of the primary pit fields and the change in relative orientation of the microfibrils in cells at different stages of extension, this concept appears to the writer to represent a probable mechanism for extension growth of coleoptile parenchyma.

Before leaving consideration of the various mechanisms of growth it is of value to consider the concept presented above in relation to those proposed by other investigators, particularly Preston and Kuyper (1951), Stecher (1952), and Roelofsen and Houwink (1953).

In investigations by Preston and Kuyper (1951) on the secondary walls of green algae, cytoplasmic aggregates were observed adjacent to the wall and from them cellulose microfibrils appeared to originate. In a more recent study of homogenized conifer cambium, Preston and Ripley (1954) have isolated what appear to be isolated aggregates of cytoplasm from which microfibrils emerge in roughly radial arrangement. These are termed by Preston and Kuyper "islands of synthesis". This concept differs from that of Stecher (1952) and from that of the present author in that it places the synthetic centre of microfibrils in the cytoplasmic surface, whereas in the former views the synthesis proceeds within the wall where it is penetrated transiently (Stecher 1952), or more permanently, by the plasmodesmata (Wardrop 1954). From an examination of the results here presented, and also those of Preston and co-workers, it would appear that actually the "islands of synthesis", at least those isolated from cambium, could correspond to isolated fragments of protoplast which *in situ* penetrated the wall in the region of a primary pit field or plasmodesm, and on homogenization separated, carrying some attached microfibrils with them. This can be seen in the case of bean root parenchyma in Plate 6, Figure 1, where what is presumed to be unextracted cytoplasm is present in a primary pit field, and from which microfibrils radiate. A similar example is seen in Plate 8, Figure 2, from conifer cambium. It is suggested that these regions *A* on isolation appear as the "islands of synthesis" described by Preston and Ripley. On such an interpretation the concepts do not appear to be as much in conflict as might at first be supposed.

A quite different mechanism—the so-called multi-net growth—was proposed by Roelofsen and Houwink (1953) initially for hair cells and elaborated in subsequent papers (Houwink and Roelofsen 1954*a*, 1954*b*) for additional cell types. In these investigations it was observed that often the orientation of the microfibrils is quite different in the outer surface of the wall from that on the inner surface. In a cell growing all over its surface, such as a cotton hair, the microfibrils are approximately transversely orientated on the inner surface and approximately axial on the outer surface. This change in orientation is attributed by Houwink and Roelofsen (1954*a*) to the extension of the wall. They further point out that, since the cells do not become thinner during extension, some relative movement between microfibrils must take place.

Irrespective of what the detailed mechanism may be, if it is accepted that extension growth does involve stretching of the cell wall, and that growth of the coleoptile involves growth controlled by endogenous auxin, then attention may be directed to the bearing of the present results on current physiological concepts of

auxin activity. It must be borne in mind, however, that, as Audas (1949) points out, growth takes place almost exclusively by absorption of water and results in a permanent increase in volume and cell wall area, while the results presented above suggest that growth involves stretching of the cell wall. Such a conclusion cannot prove or disprove any physiological concept, but only provides a line of evidence which must be taken into account when assessing the value of any physiological mechanism proposed. The main contribution of the present results is that they do not indicate that growth or auxin action involves any direct change in the nature of the entire cell wall, e.g. an effect on the non-cellulosic system of the cell wall which is demanded by a number of theories such as that of Heyn (1940). On other grounds the limitations of concepts involving direct action of auxin on the cell wall have been pointed out by Thimann and Bonner (1933). The present results impose no limitation on the idea that growth may result from water uptake by the cell, whether this uptake is osmotic or active (non-osmotic), the expanding cell surface being augmented and sustained by the intercalation of new microfibrils from the regions of plasmodesmata and primary pit fields.

It may be noted that in storage tissue there is now considerable evidence that auxin induces active water uptake by the cells. Evidence for this has been reviewed by Bonner and Bandurski (1952), and further evidence has been presented by Bonner, Bandurski, and Millerd (1953), who also point out the linkage of respiratory activity to this process. If, however, under the influence of auxin, cell elongation does result from active uptake of water, it will be clear that such mechanism imposes elongation (stretching) on the existing cell wall and presumably would involve relative movement between the microfibrils.

Evidence against the idea that active water uptake is responsible for elongation in *Avena* sections has, however, been presented in a recent paper by Ketellapper (1953), who considers that his results may best be explained on the assumption that auxin stimulates the synthesis of new microfibrils. The observation of Burroughs and Bonner (1953) that auxin favoured the formation of α-cellulose from ^{14}C-labelled sucrose, might be regarded as favouring such a view although the formation of α-cellulose was depressed when a ^{14}C-labelled acetate substrate was used. However, if auxin does serve to control, if not enhance, the formation of cell wall substances, then this synthesis could also control the increase in cell surface. Thus, if in a turgid cell the microfibrils of the microfibrillar framework are in tension and the existing microfibrils increase in length at synthetic centres (pit fields and plasmodesmata), then the stresses in the wall would be reduced and the cell permitted to resume enlargement by normal turgor forces. Such enlargement could well involve a change in orientation of the microfibrils in the region between the pit fields.

The observations presented in this paper record the change in dispersion of the cellulose microfibrils and the increasing separation of the primary pit fields in cells of increasing length. This is explicable in terms of either a simple stretching imposed on the cell wall, or a localized synthesis of material within the cell wall, which permits surface growth to occur. One further point in Ketellapper's paper which does appear to support the view that the close association of the cytoplasm

and cell wall is involved in the growth process may be mentioned. It was shown by him that plasmolysis of *Avena* coleoptile segments prior to extension in auxin reduced the subsequent elongation compared with segments not previously plasmolysed. Now it is known that on plasmolysis separation of the cell wall and the protoplast is difficult in the region of plasmodesmata (Meeuse 1941), but it is reasonable to suppose that some such connexions would be ruptured. If this occurs, then the reduced extension after plasmolysis is understandable since the number of synthetic centres within the cell wall would be reduced, leading to the reduced extension Ketellapper recorded.

While the evidence presented does not permit us to draw any conclusive picture of the nature of surface enlargement of the plant cell under the influence of auxin, it does form a basis upon which a more critical experimental approach to the problem may be planned.

IV. Acknowledgments

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Explanation of Plates 1-8

Electron micrographs in Plates 2-8 were taken at an initial magnification of ×3000 and uranium shadowed at an angle of 8°. Arrows on the electron micrographs indicate the major cell axis.

Plate 1

Fig. 1.—Parenchyma isolated by maceration from a coleoptile of *Avena*. 6 mm in length, stained with congo red, and photographed using a green filter in plane polarized light, with the plane of polarization transverse to the page. Note longitudinal band of secondary thickening and the closely crowded primary pit fields. × 430.

Fig. 2.—As Figure 1, isolated from a coleoptile 10 mm in length. Note crowding of primary pit fields. × 430.

Fig. 3.—As Figure 1, isolated from a coleoptile 70 mm in length. Note the separation of the primary pit fields. × 430.

Fig. 4.—As Figure 1, isolated from a coleoptile 17 mm in length, showing the somewhat pointed end of the terminal cell in longitudinal file. × 430.

Fig. 5.—Parenchyma cell from the peduncle of a flower of *Narcissus* sp.; aluminium shadowed at 8°. × 1000.

Plate 2

Part of the cell wall of *Avena* parenchyma isolated from stage 1 coleoptiles (Table 1) showing primary pit field. Note crowding of microfibrils. × 22,000.

Plate 3

Fig. 1.—Similar to Plate 2, showing a number of primary pit fields and crowding of microfibrils. × 18,000.

Fig. 2.—Similar to Figure 1 and Plate 2; the crowding of the primary pit fields is apparent. × 14,000.

Plate 4

Figs. 1 and 2.—Part of the cell wall of *Avena* parenchyma isolated from stage 4 (Table 1) coleoptiles showing somewhat rounded form of primary pit fields and increased dispersion of the cellulose microfibrils. Compare Plates 2 and 3. × 15,000.

Plate 5

Fig. 1.—Part of the cell wall of *Avena* parenchyma isolated from stage 5 (Table 1) coleoptiles showing increased dispersion of the microfibrils (compare Plates 2-4) and at the left a longitudinal band of secondary thickening. × 13,500.

Fig. 2.—*Pisum sativum*—Protoxylem element showing thickening bands taken 8 mm from the root tip. Compare Plate 6, Figure 2. × 18,000.

Plate 6

Fig. 1.—*Vicia faba*—Part of the cell wall isolated from the terminal 1 mm of the root. Mild maceration was used to leave most of the non-cellulosic cell wall constituents. Note the crowding of the microfibrils and what is presumably a cytoplasmic aggregate at *A* in the primary pit field. × 18,000.

Fig. 2.—*V. faba*—Part of the cell wall of a parenchyma cell isolated from the extending zone behind the tip of the root. Note the primary pit fields and dispersion of the microfibrils (compare Plate 5, Fig. 2, and Plate 6, Fig. 1). × 18,000.

Plate 7

Fig. 1.—*V. faba*—Part of the cell wall of a parenchyma cell, taken from a region 5-8 mm from the root tip where extension has ceased. Note dispersion of the microfibrils. × 15,000.

Fig. 2.—*Pisum sativum*—Part of root parenchyma from a zone in which extension had ceased. Compare Figure 1. × 13,000.

Plate 8

Fig. 1.—Part of the cell wall of a parenchyma cell from cortex of apple showing foliate texture of the cell and nearly circular primary pit fields. × 16,000.

Fig. 2.—*Pinus radiata*—Showing part of the primary cell wall of a differentiating tracheid. Note the presumably cytoplasmic aggregate with radiating microfibrils at *A*. × 12,000.

SURFACE GROWTH IN AVENA COLEOPTILE PARENCHYMA

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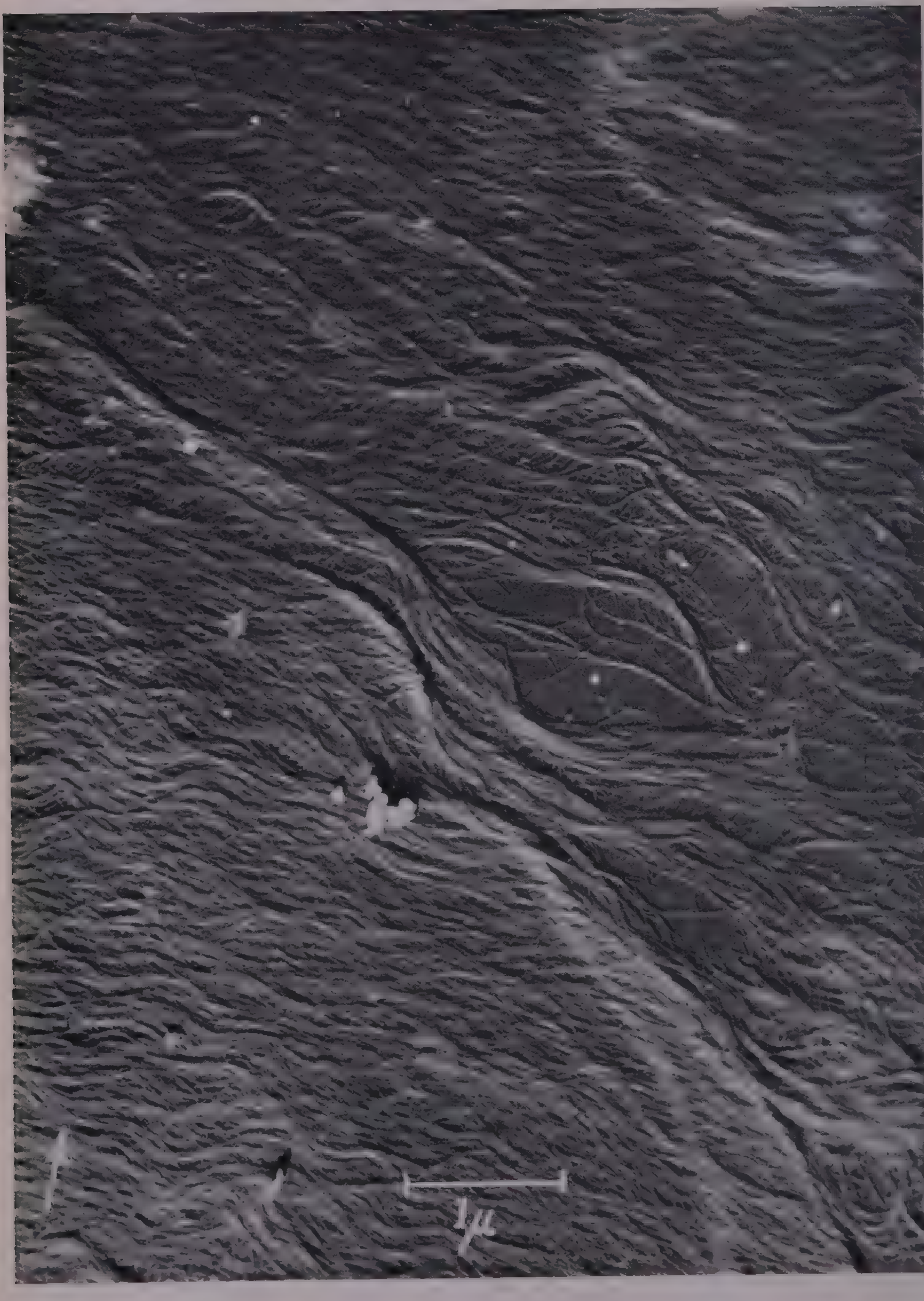

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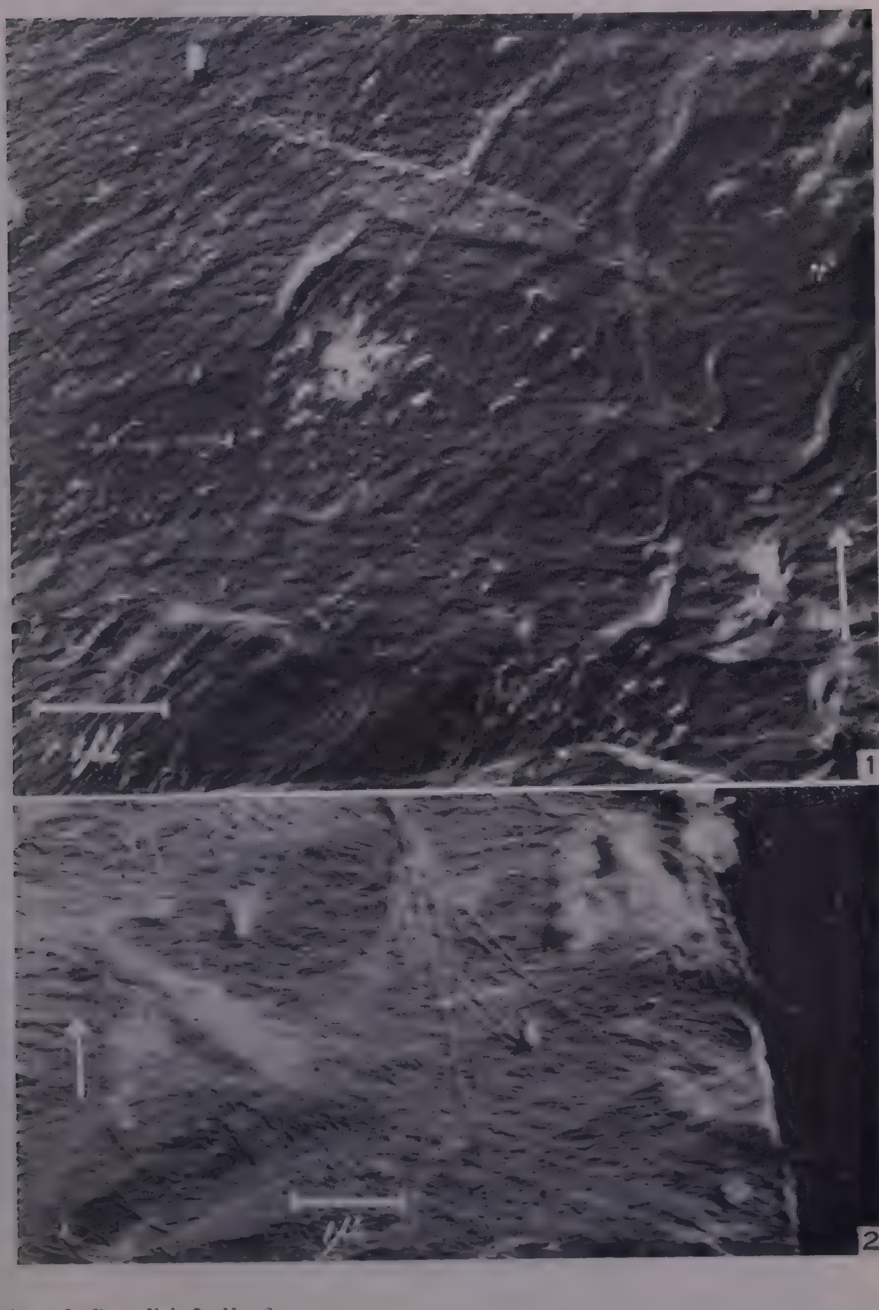

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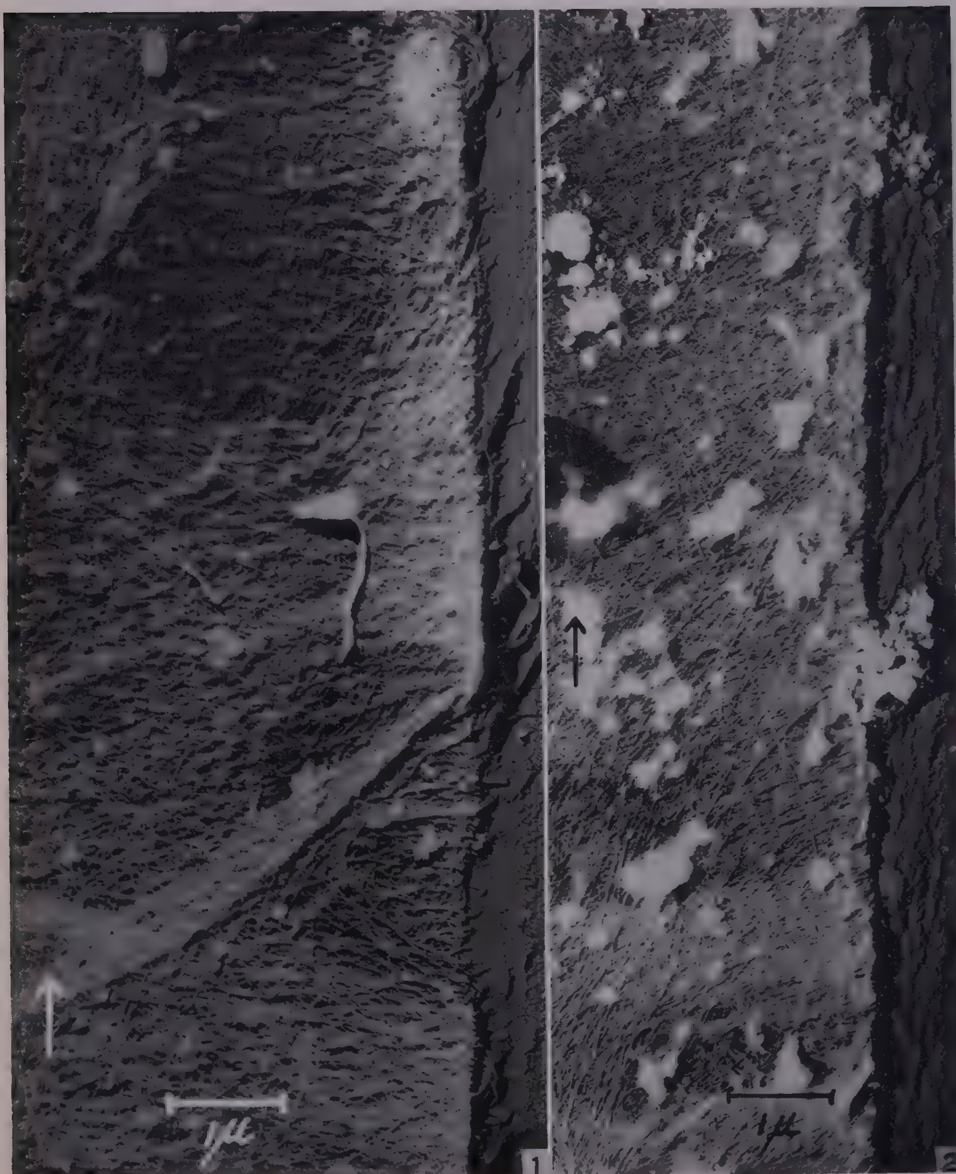

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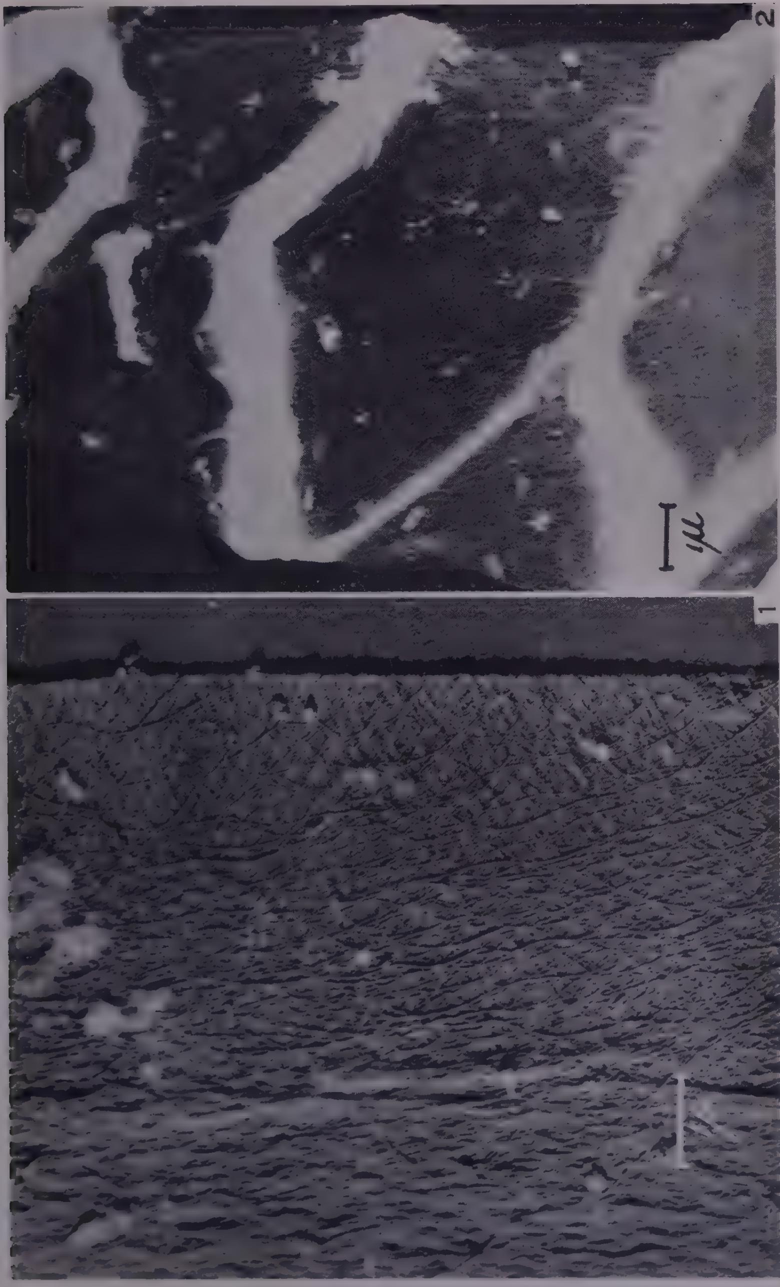

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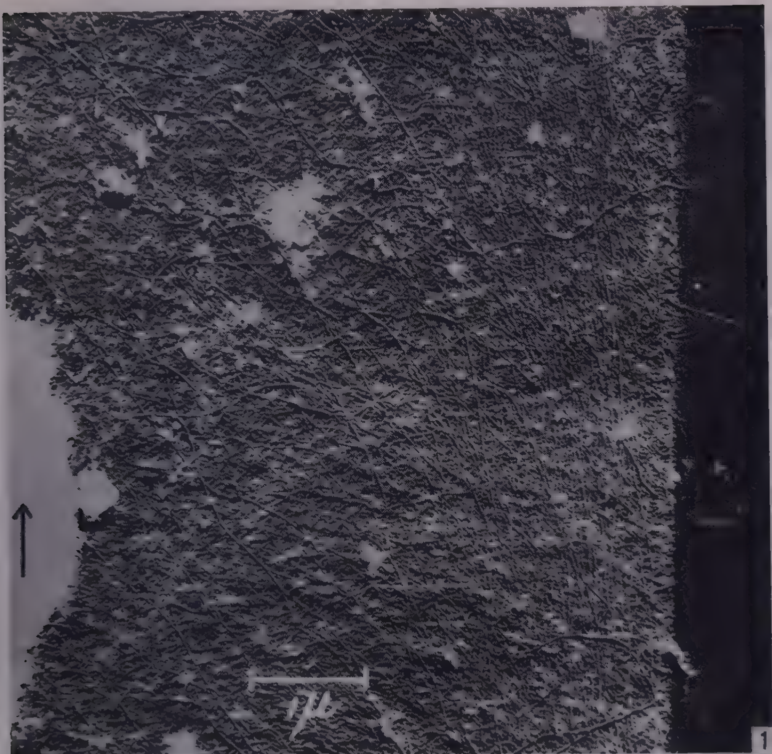

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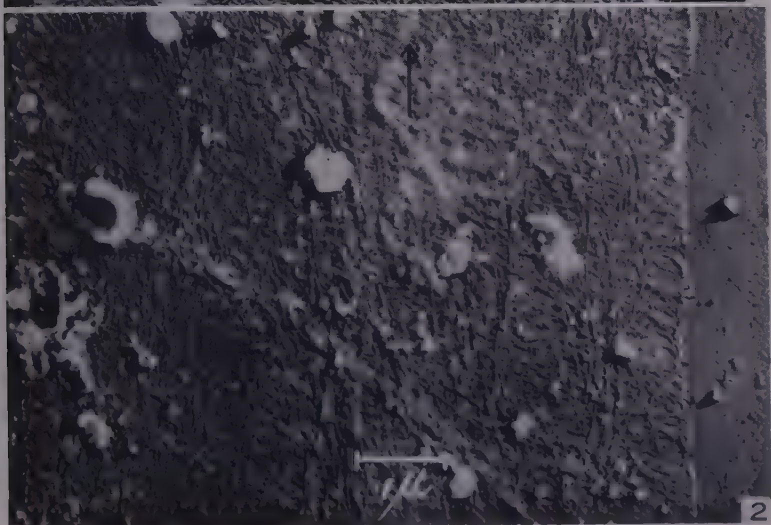

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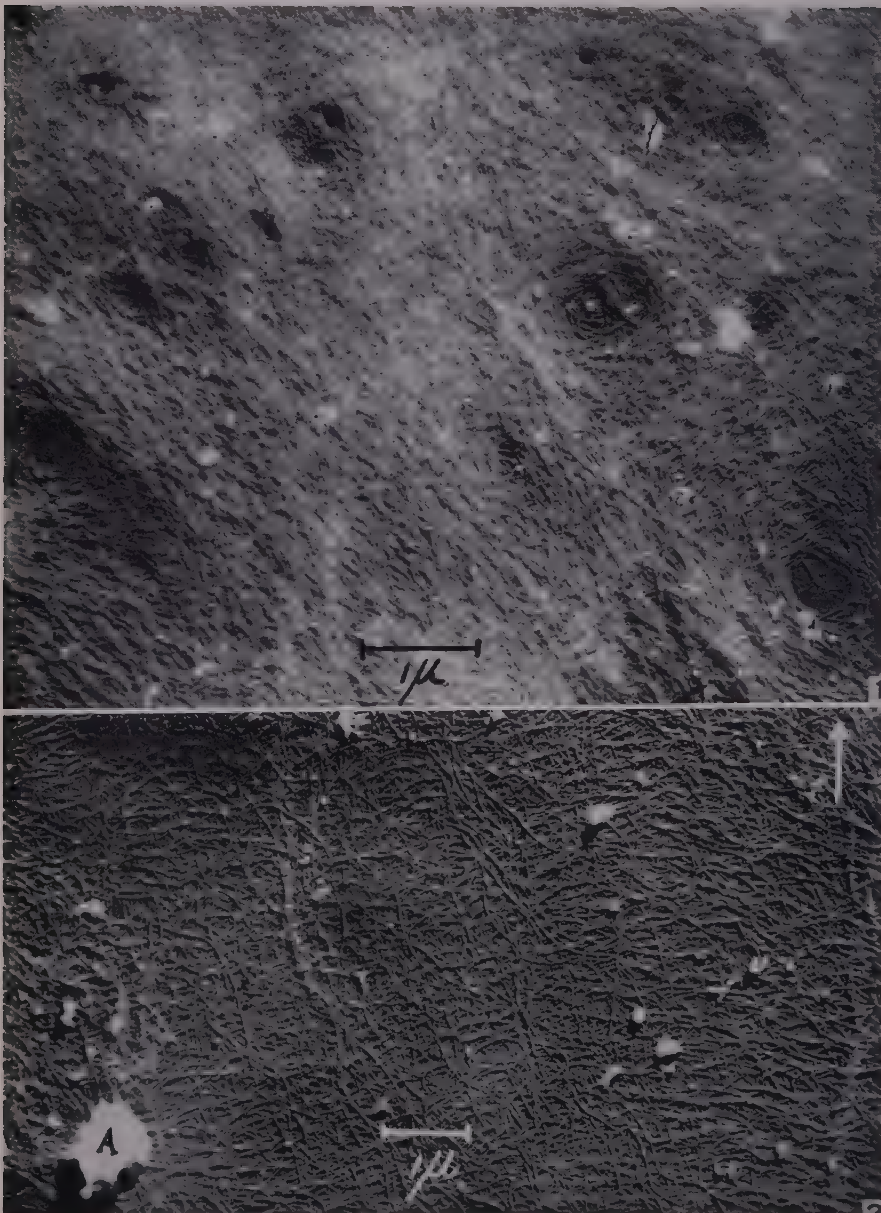
SURFACE GROWTH IN AVENA COLEOPTILE PARENCHYMA



STERILE BASE FLORETS IN *TRITICUM*

By C. Barnard*

[*Manuscript received April* 12, 1955]

Summary

The morphology of the florets in three base-sterile speltoid mutants of *Triticum aestivum* L. is described.

In two of the three mutants the basal floret only is affected. In one of these (St_1) there is a high degree of sterility in the basal floret of all spikelets except those on the distal part of the inflorescence; in the other (St_{1A}) the basal floret of the basal and the distal spikelets is nearly always fertile, the highest degree of sterility being developed in the spikelets towards the middle of the ear. In the third mutant (St_2) two florets are usually concerned. The basal floret of all spikelets except the apical one is practically always sterile. The second floret in the distal spikelets is mostly fertile, but in the lower spikelets it too is sterile and there is a gradient in fertility from distal to basal spikelets.

The minimal effect of the sterility factor is the abortion or complete suppression of the anterior stamen. This is accompanied by fusion and increased growth of the lodicule rudiments; all other floral parts develop normally. Greater incidence of the sterility results in the suppression of the lateral stamens with increased development of the lodicular structure and reduced growth of the palea. Fusion of the reduced palea and lodicular structure is usually followed by the abortion of the gynaeceum. In its extreme expression the sterility factor suppresses entirely the initiation of the flower primordium.

Failure of florets in higher positions on the spikelets to form grain is due to immaturity and is different from basal sterility.

When the basal florets are sterile, florets in higher positions than usual set grain.

The mechanism by which the *St* genes operate and the evolutionary significance of basal sterility is discussed.

I. Introduction

The report by Frankel and Fraser (1948) of the discovery of speltoid mutants of *Triticum vulgare* Host (*T. aestivum* L.) in which the basal flowers of the spikelets are missing or sterile is of considerable interest. It records for the first time the occurrence in *Triticum* of a character believed to have been of great significance in the evolution of the spikelet of the Gramineae.

There is convincing evidence of an evolutionary trend in the Gramineae towards reduction in the number of fertile florets per spikelet and the derivation of single and few flowered types from ancestral forms with many flowered spikelets (Bews 1929). This reduction is evident in the progressive loss of distal florets in some genera and of basal florets in others. Bews is of the opinion that reduction by loss of distal florets is most prevalent among the more primitive groups of grasses and that in the more advanced tribes and genera loss of the lowermost florets represents the last stage in the evolutionary trend. Basal sterility is, however, as Frankel and Fraser (1948) have pointed out, widespread in the Gramineae as a whole and they suggested that this in itself may be evidence of considerable antiquity.

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In *Triticum* the spikelet is of indeterminate growth; a number of flower primordia are formed in acropetal succession on its axis and its growing point does not terminate as a flower. From two to seven flowers are formed per spikelet but the more distal florets fail to set grain. In some randomly selected lines of *T. aestivum* L. the author (Barnard 1955) has shown that 10 or 11 flower primordia are formed on most spikelets. The distal five or six primordia, however, fail to develop beyond a rudimentary stage whilst the basal florets reach maturity. Usually only the basal two or three florets set grain but in some varieties under favourable conditions the fourth and fifth florets are also fertile. One line each of *T. dicoccum* Schubler and *T. monococcum* L. were also examined. In *T. dicoccum* four to five flower primordia are differentiated, the basal three or four developing into florets of which the two basal ones are fertile. In *T. monococcum* five to six flower primordia are formed though only the two lowermost develop into florets and the basal one alone sets grain.

There is, however, no evidence that the types with few fertile flowers in each spikelet have been derived by loss of distal florets from those species with a greater number of fertile flowers. Certainly the diploid forms *T. aegilopoides* Bal. and *T. monococcum* L., which usually bear only one fertile floret, are of greater antiquity and less "advanced" than the hexaploid and tetraploid species many of which mature two to five grains per spikelet.

McFadden and Sears (1946) conclude that the hexaploid *T. spelta* L. is an allopolyploid of the tetraploid *T. dicoccoides* Korn and *Aegilops squarrosa* L. Further they advance the hypothesis that the free-threshing hexaploids *T. vulgare* and *T. compactum* L. arose within historic time as segregates from crosses between *T. spelta* and the little Lake Dweller wheat. An origin comparable with that of *T. spelta* is postulated for the Asiatic hexaploid forms. It may be that the existing diploid and tetraploid species originated from progenitors in which a greater number of flowers were matured in each spikelet; but in the hexaploids such an evolutionary trend would have been retarded if not reversed by the influence of man's selective action since he first domesticated and cultivated this genus.

The diploid forms of *Triticum*, so far as is known, show no signs of basal sterility.* If their progenitors had a greater number of fertile florets per spikelet then reduction to the single flowered condition has been effected by abortion of the more distal florets only. It is therefore exceedingly interesting to find in a hexaploid type with more fertile flowers per spikelet the rare emergence of a base sterile factor.

From genetical studies Frankel and Fraser (1948) concluded that sterility of the basal floret in their mutants was caused by genes hypostatic to elements included in the speltoid deletion of the *C* chromosome and suggested that at least some of the hypostatic genes are situated on the *C* chromosome of *T. aestivum*.

* This sterility of the basal florets in the spikelets is not to be confused with sterility of the spikelets at the base of the spike. In most species of *Triticum* and particularly in *T. aestivum* L. the lowermost spikelets on the spike often do not develop properly and fail to mature any florets. In *T. aegilopoides* and in *T. monococcum* the terminal spikelet of the ear is abortive and barren.

The hypothesis of McFadden and Sears (1946) that *T. spelta* arose as an allopolyploid of *T. dicoccoides* and *Aegilops squarrosa* in which the *C* genome is derived from *Aegilops* suggests that the origin of the base sterile genes lies in the *Aegilops* component of the *vulgare* complex. Zhukovsky (1928), however, in his monograph on *Aegilops* does not record any base sterile types.

In the mutants of *Triticum* varying degrees of inter- and intra-spikelet sterility occur. They thus provide useful material for a study of the morphological changes involved in a process which is of considerable evolutionary significance in the Gramineae. They also present suitable subjects for a study of the mechanisms involved in this process.

In the present article a detailed description is given of the base florets, their ontogeny, and their distribution on the spike in four of the mutants. The mechanism of operation of the sterility genes is discussed on the basis of these data.

II. Material

Three of the speltoid mutants St_1, St_f, and St_2 have been described and illustrated by Frankel and Fraser (1948). St_1 was discovered in a crop of Yeoman. The basal floret of most spikelets is sterile. St_f was derived from a cross between St_1 and Victor, an unrelated variety of *aestivum*. It has speltoid characters but a high degree of fertility in the basal florets. St_2 arose from a cross between unknown Australian varieties and is quite unrelated to St_1. In St_2 not only is the basal floret of nearly all spikelets sterile but most of the second lowermost florets are also sterile.

St_{1A} is a mutant found in a crop of Fife-Tuscan which is a hybrid variety of *aestivum* resulting from a cross between Tuscan and White Fife. It is a long-awned type with speltoid characters and is similar to St_1 in that only the basal florets are sterile.

The normal types of *T. aestivum* used in this study were Yeoman, Victor, and Fife-Tuscan.

III. The Pattern of Fertility in the Normal T. aestivum Types

In Figure 1 the distribution of grain and of florets which failed to set grain is diagrammatically depicted for a typical ear of Fife-Tuscan. A very high proportion of florets in position 1 (i.e. basal position) on the spikelets form grain. This proportion progressively decreases in the florets in higher positions on each spikelet and varies with the position of the spikelet on the ear. Frequently no grain at all is formed in several spikelets at the base of the ear and less frequently in several at the tip of the ear. These spikelets, particularly those at the base of the ear, are much below normal size. Most of the infertility in flower position 1 is accounted for by the infertile florets in these basal spikelets. In the second flower position grain is not formed on these undersized spikelets nor in several basal and distal spikelets in which the first flower is fertile. Grain fails to form from florets in position 3 on spikelets further removed from the base and apex of the spike. Only on spikelets near or just below the centre of the ear are florets in the fourth position fertile.

In Figure 1 florets which failed to set grain have been classified into four grades according to their stage of development when the fertile florets are setting grain. It will be seen that the most advanced stage of development is reached at each flower position by florets on those spikelets situated near and just below the centre of the ear. The pattern of relative maturity is similar to that of the fertility of the florets and that of the order of anthesis.

POSITION OF FLOWER ON SPIKELET	TIP ← POSITION OF SPIKELET ON EAR → BASE																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	G	G	G	G	G	G	G	G	G	G	G	G	F	G	G	G	G	G	F	F
2	F	G	G	G	G	F	G	G	G	G	G	G	G	G	G	G	G	F	F	
3	F	F	F	F	F	F	F	F	G	F	G	G	G	G	G	G	F	F		
4		F	F	F	F	F	F	F	F	F	F	F	G	F	F	F	F			
5						F	F	F	F	F	F	F	F	F	F	F				
■											F	F	F	F						

G = GRAIN; F = APPARENTLY MATURE FLORETS; F = YOUNGER FLORETS WITH IMMATURE POLLEN; F = FLORETS IN WHICH POLLEN HAS NOT YET FORMED; F = VERY IMMATURE FLORETS

Fig. 1.—Diagram showing distribution of grain and florets which fail to set grain on spikelets of ear in Fife-Tuscan.

Percentages of grain formed in each flower position are given for two of the normal varieties in Table 1. The gradient in fertility between flower positions 1 and 4 is apparent. The lower fertility of the basal and distal spikelets as compared with those near the centre of the ear is also clearly seen by comparing the percentage fertility for each flower position in the columns (*a*), (*b*), and (*c*). A comparison of results for Fife-Tuscan grown under two different sets of conditions shows that in one series a smaller proportion of florets in position 3 formed grain than in the other series. There were also slightly more immature florets at position 1 in the basal and distal spikelets of this series. Victor grown under the same two sets of conditions gave similar results. In this variety, however, the difference in the proportion of immature flowers in positions 1 and 2 on the basal and distal spikelets was greater between the two sowings than in Fife-Tuscan. It is clear that environmental conditions may markedly affect the number of florets which reach maturity and form grain, although the pattern of fertility is relatively constant. Spikelets at the base and tip of the ear are most subject to environmental variation. This point is seen by comparing the results for the two sowings of Fife-Tuscan and Victor in the columns (*a*), (*b*), and (*c*) of Table 1. The difference between the two sowings is minimal when the central spikelets (column (*c*)) only are compared. With the exclusion of the distal and basal spikelets results are increasingly trimmed of the accidents of environment.

IV. Sterility in the Speltoid Mutants in Relation to Position of Floret on Spikelet

The percentage of grain formed at each flower position on the spikelets of the speltoid mutants is given in Table 1 and may be compared with the data for the normal varieties Fife-Tuscan and Victor.

TABLE 1

PERCENTAGES OF GRAIN FORMED IN RELATION TO FLOWER POSITION ON SPIKELETS IN NORMAL AND MUTANT VARIETIES

20 Ears for each variety or type

Variety	(a) In All Spikelets of Each Ear						(b) Excluding Underdeveloped Spikelets at Base and Tip of Each Ear						(c) In Five Best developed Spikelets of Each Ear*					
At Flower Position . .	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Normal:																		
Fife-Tuscan	88	74	30	—	—	—	99	84	33	—	—	—	100	97	63	—	—	—
Fife-Tuscan P†	82	72	19	—	—	—	97	85	23	—	—	—	97	99	44	—	—	—
Victor	89	82	38	6	—	—	96	88	42	6	—	—	96	96	69	12	—	—
Victor P†	71	58	22	3	—	—	97	80	30	4	—	—	98	96	62	8	—	—
Speltoids:																		
S_f	83	85	65	27	5·7	—	89	91	70	27	6	—	89	94	91	48	14	—
St_{1A}	61	89	74	31	—	—	64	94	81	32	—	—	53	95	91	57	—	—
St_1	8	85	80	44	3	—	9	90	84	46	4	—	1	93	95	77	10	—
St_2	2	27	47	36	16	0·7	6	32	57	43	16	0·8	0	24	68	60	22	1

* Spikelets 6-10 from tip of ear in St_2; 9-13 in Fife-Tuscan and St_{1A}; 10-14 in St_f and St_1; 11-15 in Fife-Tuscan P and Victor P; 13-17 in Victor.

† Grown in large pots 1954 season; remainder grown under field conditions 1954 season.

In St_f fertility of the basal flower (position 1), when the undersized basal spikelets are excluded, is slightly lower than in the normal varieties. In the second flower fertility is similar to the normal varieties, and in flowers at higher positions it is much greater. Thus St_f has either a genetically higher fertility of the upper florets than Fife-Tuscan and Victor or was more suited to the conditions of the season than these varieties. There is, not withstanding, a lower degree of fertility in the basal flowers of St_f than in the normal varieties.

In St_{1A} the fertility of the first flower is again lower than in the normal varieties whilst in St_1 and St_2 the basal flower is highly sterile. In St_2 a high proportion of flowers in the second position are sterile and even the third flower is less fertile than in the other speltoids.

TABLE 2
HIGHEST FLOWER POSITION AT WHICH GRAIN IS FORMED IN St_{1A}

Position	Grain in Position No. 1. (%)	No Grain in Position No. 1. (%)
4	45	66
3	51	34
2	4	0

A comparison of the fertility levels in the third and fourth flowers in the normal types with those in the speltoids strongly suggests that these levels rise as those of the first flower decrease. More direct evidence of this upward shift in fertility is obtained by comparing spikelets in which the base floret set a grain with those in which the base floret was infertile in the same ears. This is done for St_{1A} in Table 2. When the floret in position 1 is sterile more grain is formed at higher flower positions in the spikelet than when the basal floret is fertile.

V. Description of Sterile Base Florets

Sterile base florets are categorically different from sterile distal florets. The failure of the distal florets on all spikelets and some basal ones in the underdeveloped distal and basal spikelets in normal varieties has been attributed (in Section III) to *immaturity*. Precisely the same phenomenon occurs in the distal florets of the speltoid mutants. However, base florets in the sterile base mutants fail to set grain because of defective *differentiation* of the florets resulting in complete or partial suppression of the floret. The subtending lemma is always formed and is quite normal.

When complete suppression of the floret occurs no rudimentary structure at all is visible in the axil of the lemma at flowering time. The floret is absent and the axil of the lemma is as barren as those of the two normally empty glumes at the base of the spikelet.

When partial suppression of the floret has occurred a defective floret is present in the axil of the lemma at maturity. These defective florets have been classified into two groups for descriptive purposes and called, for lack of more apt terminology, *rudimentary* and *imperfect*. The *rudimentary* floret (Plate 1, Fig. 4) usually consists of a "palea" reduced to about one-half or one-third normal length, contorted in shape, and enclosing a gynaecial structure. Rudimentary stamens may be fused to the "palea" or occasionally patches of sporogenous tissue developed on it. Sometimes the central gynaeceum-like body has a number of stigmatic branches or consists of three or four carpelloid arms. Areas of sporogenous tissue may occur on these carpelloid segments and gradations are found which suggest that in extreme reduction the stamen rudiments assume carpelloid characters.

The flower classified *imperfect* is complete except that the anterior stamen is aborted (Plate 1, Fig. 2). Sometimes it is completely absent; sometimes present in a reduced or deformed state. When the anterior stamen is missing or reduced the lodicules are nearly always fused together and have grown into a small thin bract; when partially aborted the staminal rudiment is often fused to the fused lodicules. Flowers in which the anterior stamen has aborted may very occasionally be found in the normal varieties Victor, Yeoman, and Fife-Tuscan. Indeed, during the examination of hundreds of mature spikelets of all types abnormalities of many kinds were observed. Florets with four and five stamens in place of the usual three were occasionally encountered (Plate 1, Fig. 1). Twin spikelets, florets with two ovaries, and rudimentary florets in the axils of the normally empty glumes were also among the rarer irregularities. The abortion of the anterior stamen in an otherwise perfect floret was, however, closely associated with the sterility factor in the speltoid mutants as will be shown in Section VI. A high proportion of these *imperfect* flowers set grain.

The majority of the affected florets fall into the categories described as *imperfect*, *rudimentary*, or *absent*. Relatively few flowers occur in which the stage of reduction is intermediate between the *imperfect* and *rudimentary* types. In these not only the anterior stamen but also one of the lateral stamens is deformed or missing (Plate 1, Fig. 3). The palea is usually of normal size or only very slightly reduced and the gynaeceum appears normal. The frequency of intermediates between the *rudimentary* and *absent* categories is similarly low. In these the palea may be entirely missing and the floret represented only by a gynaceum-like structure (examples in Plate 1, Figs. 5 and 6); sometimes only a reduced and often tubular "palea" is present. This latter type is particularly common in St_{1A}.

VI. Sterility of the Speltoid Mutants in Relation to Position of Spikelet on the Ear

Frequencies of the four categories of fertility-sterility were determined for the base flower of St_1 and are graphically presented in Figure 2(*a*). Almost 90 per cent. of the first flowers of the apical spikelet are fertile. Sterility rises abruptly to 80 per cent. in the first flower of the sub-apical spikelet and then more or less gradually to the 10th spikelet from the apex. The very high sterility of approximately 98 per cent. at this point is maintained in the lower spikelets, which are not shown

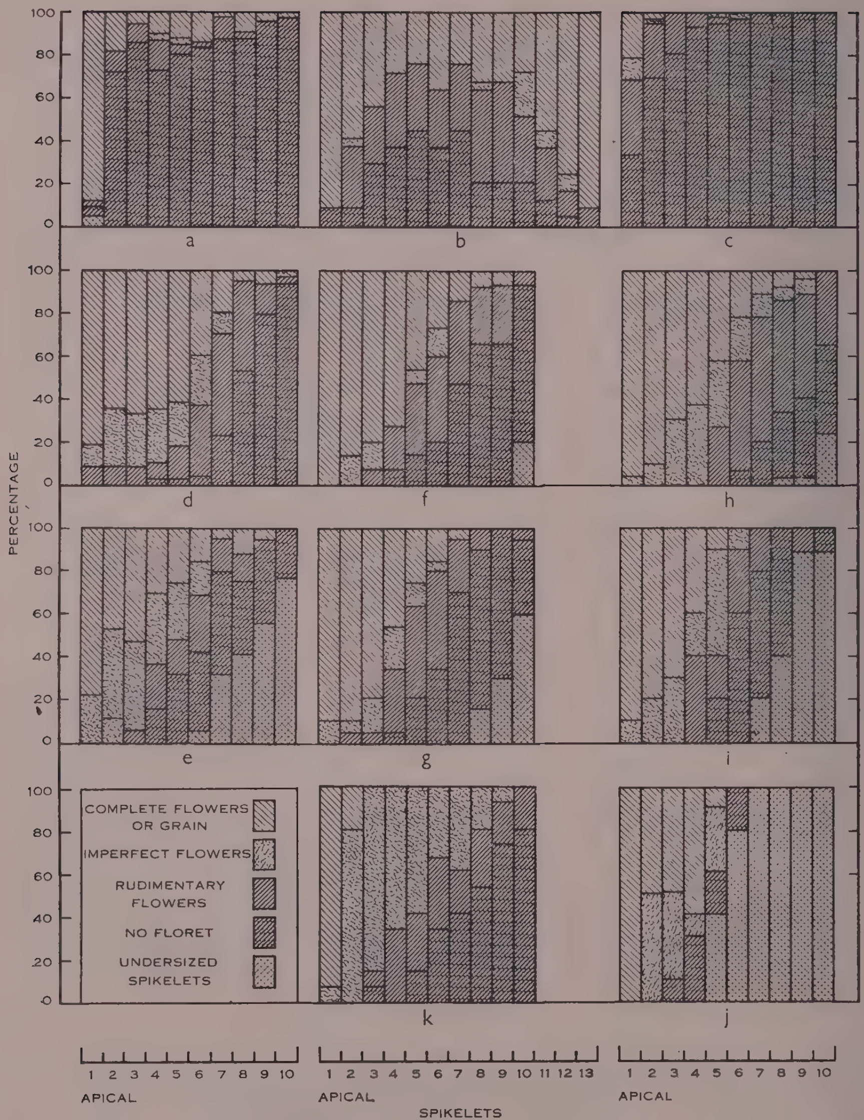

Fig. 2.—Frequency distributions of sterility-fertility categories according to position of spikelet on spike. (*a*) First flower of St_1 of the 10 most distal spikelets from 52 ears, each of which had from 21 to 23 spikelets; (*b*) first flower of St_{1A} of all spikelets from 25 ears, each of which had 12-14 spikelets; (*c*) first flower of St_2 of the 10 most distal spikelets from 59 ears, each of which had 10-11 spikelets; (*d*) second flower of St_2 of the 10 most distal spikelets from 40 large well-developed ears grown in the field; (*e*) second flower of St_2 from 19 small poorly-developed ears; (*f*) second flower of St_2 of the 10 most distal spikelets on ears of the main tiller of 15 plants grown in fertile soil in the glass-house; (*g*) second flower of St_2 from side tillers of the same plants as used for chart (*f*); (*h*) second flower of St_2 of the 10 most distal spikelets of 29 ears from plants grown in sand supplied with complete nutrient solution; (*i*) same grown in sand without phosphorus; (*j*) same grown in sand without nitrogen; (*k*) second flower of St_2 from spikes during development (c. 25-40 mm long) grown in fertile soil in the glass-house.

in the graph. In the two or three spikelets at the base of the ear, however, a very slight decrease in sterility is apparent with the occurrence of about 8 per cent. fertile or *rudimentary* florets. Throughout the spike there are relatively few *imperfect* or *rudimentary* florets, the great majority of first lemmas bearing either a complete floret or being quite empty. The second lemmas in St_1 invariably subtend a complete flower. Florets in higher positions on the spikelet develop to various stages of maturity. They are never *imperfect* or *rudimentary*.

The pattern of sterility in the first flower of St_{1A} presents a markedly different picture (Fig. 2(*b*)). The frequency of fertile florets is much higher in spikelets towards the tip and the base of the ear than in those at the centre. The number of *imperfect* or *rudimentary* flowers is much higher than in St_1. Among the *rudimentary* florets there is a high proportion in which only a small reduced and tubular "palea" is developed. The second flower in St_{1A} like that of St_1 is fertile.

The first flower of St_2 is highly sterile (Fig. 2(*c*)). Fertile flowers in the first position are almost entirely restricted to the apical spikelet. The percentage of *rudimentary* flowers is also greatest in the apical spikelet and the proportion progressively decreases to the fifth. From the sixth or seventh spikelet right to the base of the ear the first lemma is almost invariably empty.

The second flower in St_2 is also frequently sterile. Figure 2(*d*) illustrates large well-grown ears and Figure 2(*e*) small ears from the same sowing. In both a regular gradient of sterility is apparent from apex to base of the ear. The number of underdeveloped spikelets at the base of the small ears is greater than in the large ears. However, the third to sixth spikelets from the apex are comparable. Comparison of sterility in these spikelets shows a slightly greater sterility in the small ears as compared with the large ears. A similar increase in sterility is apparent when ears on the main tiller are compared with ears on side tillers from the same plants (Figs. 2(*f*) and (*g*)).

The third flower of St_2 is highly fertile except in spikelets at the very base of the ear where *imperfect*, *rudimentary*, and sometimes empty lemmas occur. Florets in higher positions on the spikelet are not affected by the sterility factor although relative immaturity limits grain formation according to the usual pattern.

The first flower of St_f is highly fertile though in the several basal spikelets *rudimentary* flowers occur. In this respect it is similar to the third flower in St_2.

VII. Basal Sterility in Relation to Environmental Conditions

It has been pointed out in Section III that the effect of environmental conditions upon the maturation of the florets and their fertility is the same in the normal and mutant varieties. The following data indicate the extent to which environmental conditions may affect the incidence of the mutant sterility factor. Data for the second floret of St_2 grown under different nutrient conditions are compared. Plants were grown in the glass-house in sand culture supplied with complete nutrient solution and solutions deficient in potassium, phosphorus, or nitrogen. The size of the ears was: complete nutrient > no potassium > no phosphorus > no nitrogen. The proportions of underdeveloped basal spikelets which are a measure of these differences are seen in Figures 2(*h*), (*i*), and (*j*). The proportion of sterile lemmas

and *rudimentary* florets for each spikelet position was: no nitrogen (Fig. 2(j)) > no phosphorus (Fig. 2(i)) > no potassium > complete nutrient (Fig. 2(h)). From these observations and the comparisons made in Section VI between small ears and large ears and main tillers and side tillers it is apparent that under environmental and particularly nutrient conditions unfavourable for satisfactory growth of the ear, the degree of "mutant sterility" of the second florets in St_2 is increased. Inadequate nutrient results in parallel effects on the mutant sterility and the immaturity sterility.

VIII. Ontogeny of the Florets

The development of the abnormal florets of the sterile mutants is described below. The morphogenesis and histogenesis of the normal floret have been previously described (Barnard 1955).

At a very early stage in the development of the spike empty or sterile lemmas may be discerned. In Plate 2, Figures 1-3, young spikes of St_f, St_1, and St_2, all of which are at approximately the same stage of development, are shown. Flower primordia are absent from the axils of the first lemma in St_1 and St_2 and from the axil of the second lemma as well in the lower spikelets of St_2. In two of the spikelets in St_2 a flower primordium is present in the axil of the second lemma though it is smaller than that present in the axil of the third lemma. These small primordia would probably have developed into *rudimentary* type florets.

Developing florets fall readily into the categories used for the mature ear. Selected types are depicted in Plate 2, Figures 4-16. The florets shown in Figures 4-11 of this plate were taken from the second flower position of spikes of St_2 *c*. 35 mm long. Figure 4 shows a perfect or complete floret from an apical spikelet; Figures 5-8 are *imperfect* florets; Figure 11 is a *rudimentary* floret from a spikelet near the base of the spike; and Figures 9 and 10 are representative of types intermediate between the *imperfect* and *rudimentary* classes.

An analysis of the distribution of these types in the material from which the photographs were derived is given in Figure 2(k). Sterility as measured by the frequency of *rudimentary* florets and empty lemmas is similar to that of the ears of the main tiller and side tillers of plants of the same series grown to maturity (Figs. 2(f) and (g)). There is, however, a very high proportion of *imperfect* florets. In the mature ears many of these would, as pointed out in Section V, have set grain and been classified as fertile.

Plate 2, Figures 12-16, shows perfect, *imperfect*, and *rudimentary* type florets at a younger stage.

In the *imperfect* type floret the anterior stamen is usually missing altogether and the two lodicules are fused (Plate 2, Figs. 7, 8, and 14). The lodicules are rarely normal when the anterior stamen is missing. From sectioned material it is evident that some periclinal divisions may take place in the cells of the sub-hypodermis in the usual manner (Barnard loc. cit.) initiating stamen differentiation. Such merismatic activity may cease after a few divisions or may become incorporated in the merismatic activity initiating the lodicules. Merismatic activity generally continues along the whole length of the small ridge of tissue on the

anterior side of the flower primordium giving rise to a single lodicular structure. In normal flower primordia merismatic activity is restricted at a very early stage to a point at each end of the ridge from which the growth of the two lodicules proceeds (Barnard loc. cit.). It is clear that when the anterior stamen is missing in the mature floret this is not the result of abortion during development but of failure of a rudiment to differentiate from the flower primordium.

Sometimes the rudiment of the anterior stamen is present but is improperly differentiated and much smaller than those of the normal lateral stamens (Plate 2, Figs. 5, 6, and 13). These primordia develop into florets with the anterior stamen deformed.

Florets in which one of the lateral stamens fails to form, or in which both lateral stamens though clearly recognizable fail to develop properly, occur less frequently. Examples of such florets are pictured in Plate 2, Figures 9 and 10. In these types the gynaeceum usually appears normal. Characteristically the lodicules are fused and form a single, entire or bifid structure as large as and thicker than the developing palea.

Florets which in the mature ear have been classified *rudimentary* are also readily distinguishable at a very early stage of development. The single lodicular structure is often better developed than the palea and fused with it to form a continuous envelope (Plate 2, Figs. 11, 15, and 16). It is safe to conclude that in the majority of florets classified *rudimentary* in the mature ear the structure described as a reduced and contorted "palea" (Section V) is in reality the fused palea-lodicule with the lodicule component predominating. Frequently the segments of the lodicular structure are covered with large secretory cells giving them a stigmatic appearance. Staminal rudiments often also present a carpelloid appearance. When staminal rudiments are entirely absent the carpel rudiment is present as a continuous ring of tissue encircling the growing point (Plate 2, Figs. 15 and 16). In Plate 4, Figure 4, a longitudinal median section of a floret comparable to that depicted in Plate 2, Figure 10, is shown. No stylar tissue has developed in the carpel, which consists of an ovary portion and encloses the growing point of the flower primordium. Plate 4, Figure 3, shows another floret of the *rudimentary* type in which the parts have not differentiated properly. Compare Barnard (loc. cit.), Plate 4, Figure 6.

It is thus evident that the abnormalities observed in the *imperfect* and *rudimentary* type florets at maturity arise during the differentiation of parts in the flower primordium.

Lemmas which at maturity have no discernible structure in their axils and which were classified in Sections V and VI as empty may or may not have subtended a flower primordium in their early stages of development. A flower primordium may form but fail to develop and cease growth before any differentiation of parts occurs. Such primordia may only be discerned during and for a short period after their formation. Examples are shown in Plate 2, Figure 3, in Plate 3, Figure 4, and in Plate 4, Figures 1 and 2. On the other hand there may be no indication of the differentiation of any axial structure at all. A longitudinal section of a very young spikelet of St_2 in which the third lemma has just formed

is shown in Plate 3, Figure 2. There is no sign in the axil of either the first or second lemma of the characteristic periclinal divisions in the sub-hypodermis (Barnard loc. cit., Fig. 6) which indicate flower primordium initiation. An apical spikelet of St_1 with the third lemma arising is illustrated for comparison in Plate 3, Figure 1; it shows that normally quite a large flower primordium is developed in the axil of the first lemma at this stage and a small one is forming in the axil of the second lemma.

Flower primordia which abort before the initiation of any flower parts are smaller in size than normal primordia at comparable spikelet positions; the difference in size depends upon the stage reached when abortion commences. Such primordia are recognizable most clearly in section by the loss of merismatic activity, vacuolation, and lighter staining of their cells. At the stage when stamens and carpel are being initiated there may be little difference in size between those primordia which are differentiating these parts properly and those which are not. By the time the flower primordia have differentiated sufficiently to permit recognition of their ultimate form (younger than those of Plate 2, Figures 12-16) the size of those primordia which will develop into *rudimentary* type florets is considerably less than that of the normal florets at comparable positions on the spikelet. Examination of spikelets at many stages of development indicates that the rate of growth of the *rudimentary* type floret is dependent upon the degree of differentiation of floral parts. The *imperfect* type florets on the other hand develop at approximately the same, if not the same, rate as the normal florets.

IX. Discussion

It has been shown that the sterility of the base florets in the speltoid mutants is different in origin from the sterility of the distal florets which occurs in both the speltoid types and normal varieties. The sterility of the basal lemma in the speltoids results from failure of a flower primordium to form or to differentiate its floral parts.

In Figure 3 the development of some of these defective florets is diagrammatically illustrated. All categories of defective florets have their origin during the period of floral organogenesis; their subsequent growth is dependent upon the degree of differentiation of parts attained during this period. Flower primordia which fail to differentiate any parts abort. On the other hand organogenesis of florets which fail to set grain in the higher positions on the spikelet is normal; these florets are perfect in form. Because the development of the florets on the spikelet axis is acropetal the distal florets have not reached maturity at the time of general anthesis in the ear and therefore do not set grain.

Fraser (1950) formulated a hypothesis to explain the mechanism of the base sterile factor in the speltoid mutants. He postulated the presence of an activator which controls the growth of differentiated flower primordia. This activator only has an effect when its concentration exceeds a certain threshold level. In the sterile mutants it failed to reach threshold value during the "sensitive periods" of the basal florets. Fraser, however, assumed that the base sterility was comparable in origin with the "sterility" of the upper florets which failed to set grain.

If one must postulate control by the *St* genes of a substance which activates or inhibits the formation and differentiation of flower primordia then the following conditions may be chosen to accord with the observed morphogenesis:

(*a*) The substance is concerned primarily with the initiation of structures having a cauline origin (i.e. the flower primordia and stamen initials (Barnard 1955)) rather than with those which arise from the dermatogen and hypodermis in the manner of a foliar structure (i.e. palea, lodicules, carpel).

(*b*) Each site of origin of a cauline structure on the spikelet and floral axes receives only a certain amount of the activator which is consumable; or a higher concentration is required by each succeeding locus of differentiation.

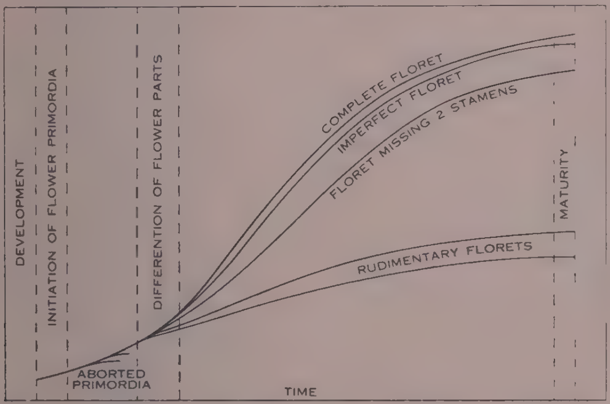

Fig. 3.—Diagram of development of complete and defective florets.

(*c*) The differentiation of an organ extends over a limited period of time, i.e. individuation occurs whilst the primordium is still very small.

(*d*) The supply of the activator is inhibited by the *St* genes during early development of the spikelet.

If we assume that the mechanism involves the presence of an activating substance of the above nature, then—where the site of origin of a flower primordium received none of the activator—no primordium is formed: where an inadequate ration is received a *rudimentary* type floret is formed; whilst an almost full quota gives rise to an *imperfect* floret. In the case of the *imperfect* floret the amount of activator received has been sufficient to differentiate the flower primordium and sufficient has remained to differentiate properly the lateral stamen initials. The substance is expended, however, before the initiation of the anterior stamen, which is the last structure of cauline origin to form on the floral axis (Barnard 1955). Where the site of origin received only a very small amount of the stimulating substance, initiation of the flower primordium takes place but abortion ensues before individuation is attained. With a slightly greater amount of the activator the primordium may just reach the stage when differentiation of its parts commences. Because of lack of the "cauline" activator, stamen initials fail to develop or abort

at a very early stage. The primordium for the same reason is inadequate as an axis upon which the structures of foliar origin, the palea, lodicules, and carpel, can develop properly. Hence these structures though differentiated fail to grow normally to full size. The morphogenesis of floral types intermediate between the categories of absent, *rudimentary*, and *imperfect* may be similarly interpreted. This hypothesis does not offer any explanation for the abnormal development of the lodicular structures. The fusion of the two lodicules and the fusion of the lodicules with the palea on the other hand is probably only an indirect effect of the *St* genes as the phenomenon of the fusion of adjacent organs is frequently associated with morphological reduction.

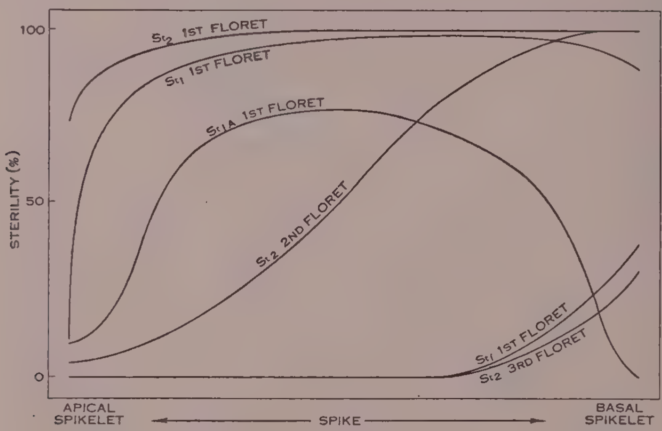

Fig. 4.—Diagram showing relation of basal sterility to position of spikelet on ear.

In each type of mutant, basal sterility is expressed in a well-defined pattern on the spike or ear (Section VI). In Figure 4 these patterns are illustrated diagrammatically.

The fact that sterility in the basal florets of the speltoid mutants was associated with an increased fertility of florets at higher positions on the spikelet would at first sight appear inconsistent with Bews' view (see Section I) that reduction in the number of effective florets per spikelet results from the loss of basal florets. If the number of florets per spikelet were already limited by the genetic abortion of its distal florets such a compensating effect would not be possible. Under conditions of environmental stress the most distal florets of the spikelet, as has been observed in *Triticum*, fail to reach maturity. This is probably a direct nutritional effect. Adaptation to less favourable environmental conditions could be accompanied by a genetic abortion of the distal florets. Reduction in the number of florets per spikelet from the base could then represent the last stage in an evolutionary trend.

The sequence and nature of the morphological aberrations in the speltoid wheats are, so far as is known, different from those associated with basal sterility

in other genera of the Gramineae. In the subfamily Panicoideae where base sterile florets occur in all genera the spikelet consists of a perfect flower with a male floret or empty lemma below it. In the subfamily Pooideae basal florets in which the gynaeceum is suppressed and empty lemmas are also found. The evidence suggests and it is generally held that the male floret represents an intermediate state in the degeneration of the floret which ultimately results in the empty lemma condition. There is, however, no evidence that this empty basal lemma condition, which is so widespread in the Gramineae, has resulted from a process involving the abortion of the stamens before the gynaeceum or in abnormal lodicule development. Study of the occurrence and morphogenesis of intermediate type florets in many genera is required before this point may be adequately decided. Such studies are in progress.

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Explanation of Plates 1-4

Plate 1

Complete, *imperfect*, and *rudimentary* florets from mature ears of St_2 speltoids.

Fig. 1.—A complete or perfect floret and an abnormal one with five stamens. × 7·1.

Fig. 2.—*Imperfect* florets showing anterior stamen absent or aborted (*as*) and presence of bract-like lodicule (*lo*). Lodicule removed from second floret. p = palea. × 7·1.

Fig. 3.—Florets intermediate in development between *imperfect* and *rudimentary* types, with only one lateral stamen developed and bract-like lodicule (*lo*). × 7·1.

Fig. 4.—Typical *rudimentary* type florets with reduced "palea" like contorted envelope surrounding gynaecial structures. × 7·1.

Fig. 5.—Small *rudimentary* type florets. × 7·3.

Fig. 6.—Small *rudimentary* type florets; the example in the centre has no enclosing envelope. × 8·9.

Plate 2

Dissections illustrating floral development in the speltoid mutants.

l_1 = first lemma; l_2 = second lemma; *fp* = flower primordium; *lo* = lodicule; *as* = anterior stamen; *ls* = lateral stamen; p = palea; c = carpel.

Fig. 1.—Spike of St_f. The third lemma is arising in most spikelets and a flower primordium with parts differentiating is present in the axil of all basal lemmas. × 24.

Fig. 2.—Spike of St_1 in which the fourth lemma is arising and all basal lemmas are empty. × 22.

Fig. 3.—Spike of St_2 on which the fifth lemma is arising on the most advanced spikelets. The first lemma is empty on all spikelets. The second is empty on the three lowermost spikelets. In the axil of the second lemma in the third and fourth spikelets from the base a small aborting flower primordium is present whilst in the sub-apical spikelet a flower primordium in the axil of the second lemma is developing properly. × 22.

Fig. 4.—A perfect floret well developed. × 55.

Fig. 5.—An *imperfect* floret in which the lodicules are fused and a small knob rudiment represents the anterior stamen. × 37.

Fig. 6.—An *imperfect* floret in which the lodicules are fused and the anterior stamen is a small bract-like structure. × 37.

Fig. 7.—An *imperfect* floret with anterior stamen missing and lodicules fused. × 37.

Fig. 8.—A younger *imperfect* floret, lodicules fused and no anterior stamen. × 34.

Fig. 9.—Floret with large lodicular structure, one lateral stamen and gynaeceum properly developed; second lateral stamen as rudiment. × 42.

Fig. 10.—Floret with palea and lodicular structure; anterior stamen missing and two lateral stamens abortive; gynaeceum normal. × 27.

Fig. 11.—Floret in which large bifid lodicular structure is fused with palea with a gynaecial structure probably enclosed. × 29.

Fig. 12.—A small perfect floret before palea has grown up. × 58.

Fig. 13.—A small *imperfect* floret with a *rudimentary* anterior stamen but lodicules normal. × 44.

Fig. 14.—A very small *imperfect* floret before palea has grown up, with fused lodicules and anterior stamen missing. × 60.

Fig. 15.—A *rudimentary* type floret in which a bifid lodicular structure is opposed to a palea with the rudiment of one lateral stamen showing and the carpel developed as ring or ridge of tissue around growing point. × 35.

Fig. 16.—A *rudimentary* floret similar to Figure 15; no staminal rudiments evident. Enclosing tube of lodicule-palea. The inner ring of tissue represents the carpel. The growing point of the floral axis is in the centre. × 33.

Plate 3

Longitudinal sections of spikelets of base sterile wheats.

l_1 = first lemma; l_2 = second lemma; l_3 = third lemma; *fp* = flower primordium.

Fig. 1.—Young terminal spikelet of St_1 with third lemma forming; a flower primordium with anterior stamen differentiating is in the axil of the first lemma and a flower primordium is arising in the axil of the second lemma. × 175.

Fig. 2.—A young spikelet from the base of a spike of St_2. The third lemma is arising and no flower primordium is forming in the axils of the first or second lemmas. × 158.

Fig. 3.—A terminal spikelet of St_1 in which the sixth lemma is arising. Normal flower primordia with parts differentiated in axils of both first and second lemmas. × 102.

Fig. 4.—A spikelet of St_2 in which the sixth lemma is forming with a small aborting flower primordium in the axil of the first lemma and a normal flower primordium in the axil of the second lemma. × 113.

Plate 4

Longitudinal sections of spikelets and flower primordia of base sterile wheats.

l_1 = first lemma; l_2 = second lemma; *p* = palea; *lo* = lodicule; *as* = anterior stamen; *c* = carpel; *gr* = growing point.

Fig. 1.—A spikelet of St_1 in which sixth lemma is forming and a very small aborting flower primordium is in axil of first lemma. The second lemma subtends an imperfect primordium in which the carpel is forming but the anterior stamen has failed to develop. × 113.

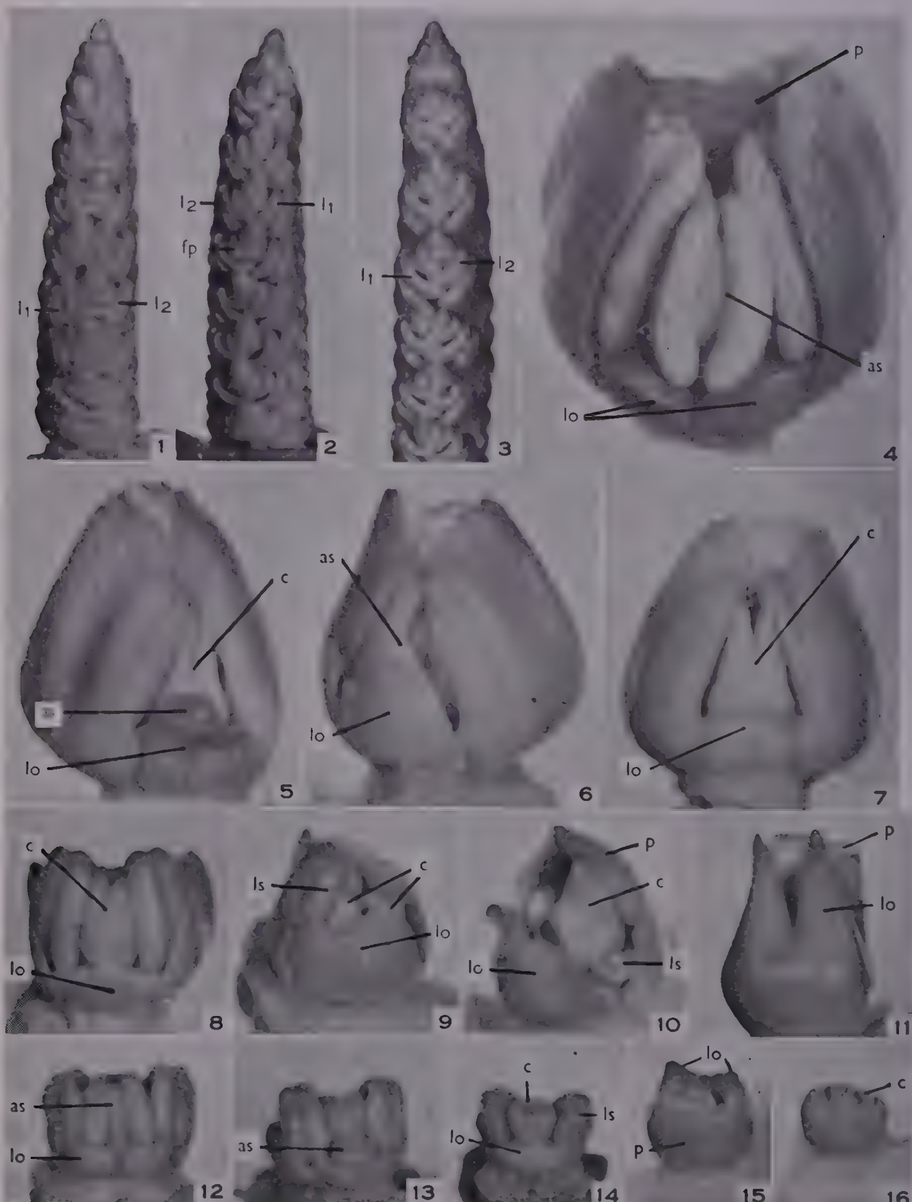
Fig. 2.—A spikelet of St_2 from toward the base of the spike. The sixth lemma is forming; the first lemma is completely sterile and the second subtends a very small aborting primordium. × 114.

Fig. 3.—A flower of the *rudimentary* type from St_2 showing palea, lodicular bract, and four rudiments below the growing point of the primordium. One of these rudiments is staminoid. × 160.

Fig. 4.—A very *rudimentary* type floret in which the palea and a large lodicular structure surround the carpel. × 248.

STERILE FLORETS IN TRITICUM

STERILE FLORETS IN TRITICUM



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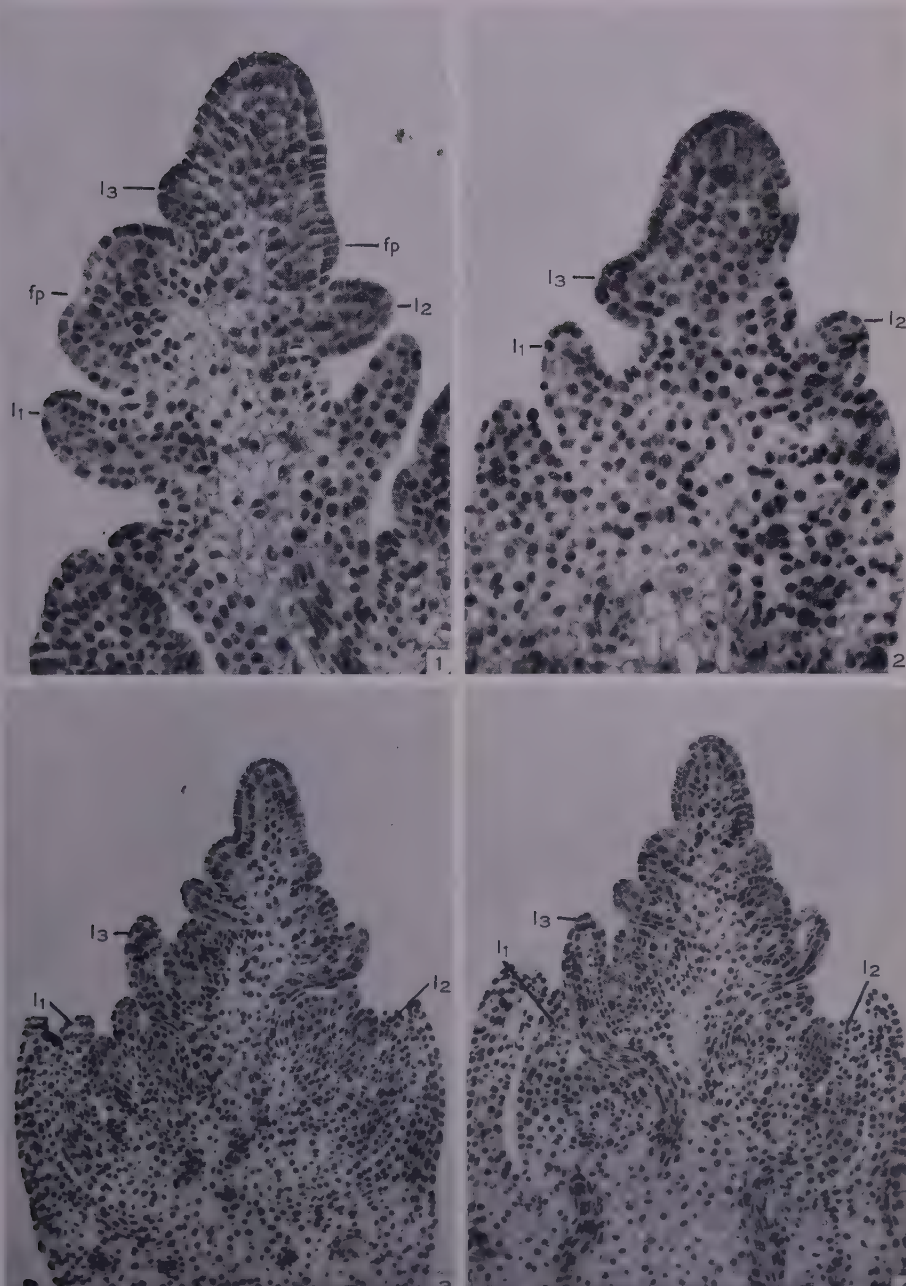

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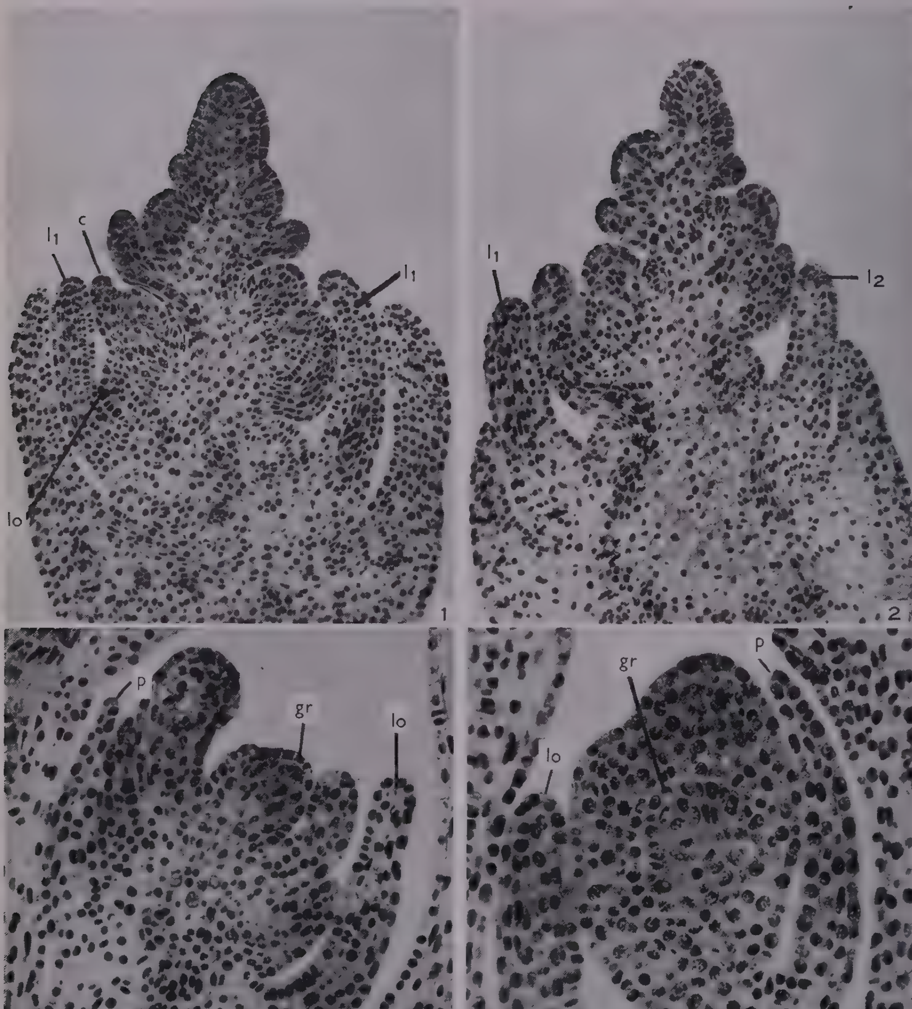

THE ANATOMY OF BARK

V. EUCALYPTUS SPECIES WITH STRINGY BARK

By M. MARGARET CHATTAWAY*

[*Manuscript received January* 18, 1955]

Summary

The term "stringybark" has been applied to certain rough-barked eucalypts in which the outer bark is persistent, loose, and fibrous. This texture arises through the expansion of the phloem parenchyma, which causes the bundles of fibres to become widely separated from one another in the rhytidome.

This expansion, which may increase the cells to many times their original size, takes place after the periderm has formed, and immediately precedes the death of the cells and their transformation into rhytidome.

This feature is not confined to the series Pachyphloiae (stringybarks) but also occurs in several related series, and in some of the rough-barked bloodwoods.

I. INTRODUCTION

In many rough-barked species of *Eucalyptus* there may be considerable growth outside the periderm, so that the pattern of tissues in the rhytidome is very different from that of the outer phloem. This pattern comes from the formation of new tissue by division of the phellogen or from changes in the pattern of the phloem by growth in the still meristematic parenchyma of the outer phloem. In certain species both these processes occur and the resultant rhytidome bears very little resemblance to the tissues of the living phloem (Plate 1, Figs. 1 and 2).

It has been found that changes that result in the ultimate death of a cell can in their initial stages cause increased activity, producing cell growth to an abnormal extent and resulting in an increase in size to many times that of the original cell. In woody tissues this causes tyloses to form after injury or at the onset of heartwood formation (Chattaway 1949); in the phloem it finds expression in this enlargement of the rhytidome parenchyma to give a loose fibrous tissue which has led to the vernacular name of "stringybarks" for some species of *Eucalyptus*.

II. MATERIAL

Typical "stringybark" rhytidome occurs in the following species; the classification is that of Blakely (1934), and the numbers in brackets refer to the number of samples available for examination.

Stringybarks

PACHYPHLOIAE: *E. agglomerata* Maid. (10); *E. baxteri* (Benth.) Maid. & Blakely (9); *E. blaxlandi* Maid. & Cambage (2); *E. caliginosa* Blakely & McKie (4); *E. cameroni* Blakely & McKie (13); *E. capitellata* Sm. (2); *E. fastigata* Deane & Maid. (7); *E. globoidea* Blakely (4); *E. laevopinea* R. T. Bak. (10); *E. macrorrhyncha* F. Muell. (9); *E. obliqua* L'Herit. (22); *E. regnans* F. Muell. (33); *E. scabra* Dum-

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Cours (9); *E. tindalae* Blakely (2); *E. wilkinsoniana* R. T. Bak. (4); *E. youngmani* Blakely & McKie (2). Twenty-two species were not available for examination.

PSEUDO-STRINGYBARKS: *E. pilularis* Sm. (9); *E. muelleriana* Howitt (6). One species was not available for examination.

Species with More or Less Well-developed Stringy Barks

CORYMBOSAE: *E. abbreviata* Blakely & Jacobs (1); *E. abergiana* F. Muell. (5); *E. dichromophloia* F. Muell. (8); *E. setosa* Schau. (2). Three species were not available for examination.

CORYMBOSAE-PELTATAE: *E. gummifera* (Gaertn.) Hochr. (6); *E. intermedia* R. T. Bak. (3); *E. polycarpa* F. Muell. (7); *E. trachyphloia* F. Muell. (2). Five species were not available for examination.

TRANSVERSAE: *E. botryoides* Sm. (9); *E. jacksoni* Maid. (3); *E. kirtoniana* F. Muell. (1); *E. major* Blakely (6); *E. pellita* F. Muell. (25); *E. resinifera* Sm. (9); *E. robusta* Sm. (11). Two species were not available for examination.

ARGYROPHYLLAE: *E. cephalocarpa* Blakely (3); *E. cinerea* F. Muell. (4). Four species were not available for examination.

DIVERSIFORMAE: *E. todtiana* F. Muell. (4). Two species were not available for examination.

OCCIDENTALES: *E. marginata* Sm. (4). Three species were not available for examination.

WHITE MAHOGANIES: *E. umbra* R. T. Bak. (1); *E. carnea* R. T. Bak. (2); *E. triantha* Link (8). One species was not available for examination.

STEATOXYLON: *E. microcorys* F. Muell. (8).

FRAXINALES: *E. gigantea* Hook. f. (8); *E. planchoniana* F. Muell. (11). Twelve species were not available for examination.

III. Description

Expanded rhytidome parenchyma has already been briefly described and figured (Chattaway 1953). It is most constant and conspicuous in the series Pachyphloiae (stringybarks), where it occurs to some degree in all the rough-barked species examined. It was developed to some extent in all samples of the 14 species examined, except in *E. obliqua*, *fastigata*, and *regnans* (rough basal parts only). In these three species there were some samples from which it was entirely absent, but there was not sufficient material to say whether this was merely a local variation or whether it applied to all parts of the trunk.

A further feature of these stringy barks is the presence of wide bands of thick-walled, lignified phellem, in which the thickening is usually greater on the inner side of the cells (Chattaway 1953, Fig. 7). It can be seen as a broad band of tissue in Plate 2, Figures 1 and 2. The cells that form this tissue are present in all species of *Eucalyptus* examined, but their maximum development seems to be associated with the loose-textured stringybark rhytidome. They appear to offer considerable resistance to abrasion and form the outer layer of all smooth-barked trees; in the stringybarks they form a strongly cohesive tissue, holding together the layers of looser expanded rhytidome.

There is considerable variation in the amount of expansion and in its distribution (Plate 1, Figs. 3 and 4; Plate 2, Fig. 3); the greatest amount observed represented a radial increase of about 30 times the original diameter of a cell, all of this increase occurring after the periderm had formed. Sometimes the expansion is consistently great through a number of successive rhytidome layers, sometimes it is localized in one or two, and sometimes it occurs in several layers which are interspersed with unexpanded ones (Plate 2, Fig. 3).

IV. Discussion

With the exception of a few bloodwood species the series with loose stringybark structure in the rhytidome form a closely related group; they include species from Blakely's series IV and V (Corymbosae and Corymbosae-peltatae), XXI (Argyophyllae), XXIII and XXIV (Diversiformae and Occidentales), and XXVI to XXX (Pseudostringybarks, White Mahoganies, Tallowwoods, Stringybarks, and Fraxinales). Expanded rhytidome has only been found in conjunction with oil glands in two species (Chattaway 1955*a*), *E. cephalocarpa* and *cinerea* of the Argyrophyllae (Plate 2, Fig. 4). It is often associated with radially elongated phelloderm (Chattaway 1955*c*). It has not been observed in the peppermints, boxes, or ironbarks, though all these groups have thick persistent rhytidomes. In the peppermints there is very little growth outside the periderm; in the boxes and ironbarks any growth that does occur is usually confined to the phellem and is a new tissue, formed by divisions of the phellogen and not by a size increase of existing parenchyma cells.

The rough-barked bloodwoods are a group of species with unusual phloem features (Chattaway 1953, 1955*b*). The bundles of large phloem fibres form a relatively compact inner phloem; they become separated by growth of the parenchyma cells in the outer phloem. In a few species the expansion of the parenchyma outside the periderm is of quite an irregular nature—a slight extension of the growth in the outer phloem, with only occasional patches showing radial expansion. However, in the species listed above (Corymbosae and Corymbosae-peltatae), there is an approach to the typical stringybark rhytidome (Plate 1, Fig. 5; Plate 2, Fig. 5). The expansion is seldom as great as in the true stringybark species, and produces a flaky- rather than a stringy-textured bark.

The enormous and sudden expansion that takes place in the stringybarks must occur rapidly, as the full cell size is often attained in the first layer of rhytidome (Plate 1, Figs. 3 and 4). These radially expanded parenchyma cells differ in position and in structural details from the radially elongated parenchyma found in other types of bark. Radially elongated parenchyma occurs in the outer phloem of *E. maculata* Hook. (Chattaway 1953, 1955*b*) and some other smooth-barked bloodwoods, but it is formed under different conditions, in the living phloem, and is characterized by having thickened walls and conspicuous bordered pits. The radially elongated phelloderm cells previously described (Chattaway 1953, 1955*b*) are also part of the living phloem, for though they develop after periderm formation they are on the inside of the periderm, and they too are usually characterized by their conspicuous bordered pits, and by the often very heavy sclerosis of their

walls. Such cells have been formed from the meristematic phloem parenchyma by a growth that is not merely expansion, but involves the laying down of secondary thickening by an actively living cell.

It has been shown that the onset of death can upset the cell metabolism and cause an increase of growth and secretion. Thus in the xylem the ray cells can grow to many times their normal size to form tyloses shortly before their death and consequent transformation to heartwood (Chattaway 1949). A similar disturbance of the cell metabolism occurs when the outer layers of the phloem are cut off by the periderm. Their food supply is gradually cut off and they are destined to die. A great burst of cell activity occurs which shows itself in the enlargement of the thin-walled parenchyma cells of the outer phloem to form the enlarged cells of the rhytidome.

Pits are very seldom observed either in the phloem parenchyma or in the expanded rhytidome cells, and the explanation is probably the same in both cases. These cells undergo only the slightest secondary thickening; before periderm formation the phloem parenchyma cells are still meristematic and without secondary thickening, though a few of them may enlarge and form thin-walled stone cells in which numerous pits can be seen. On periderm formation the stone cells remain unchanged and can be found here and there scattered throughout the rhytidome. A comparison of stringybark phloem with that of other eucalypts under polarized light shows that, whereas secondary thickening is always absent from parenchyma of the inner phloem, in the stringybarks this condition persists throughout the phloem; and at the periphery there are still, at the time of periderm formation, very few parenchyma cells with secondary thickening. The cells of the phloem are therefore still in a stage at which they can undergo expansion. They become very slightly thickened and lignified in the outer layers of the rhytidome, the amount apparently depending on the length of time which elapses before they are killed by the completion of the periderm and the loss of food supplies. In no case have they been observed to have walls of a thickness comparable with those of the sclerosed phelloderm. Even in *E. obliqua*, in which the radially elongated phelloderm cells are commonly very thin-walled and the rhytidome parenchyma only slightly expanded, a great difference in the degree of thickening can be observed under polarized light.

V. Acknowledgments

The author wishes to acknowledge her indebtedness to all who have helped by sending material, cutting sections, and in many other ways.

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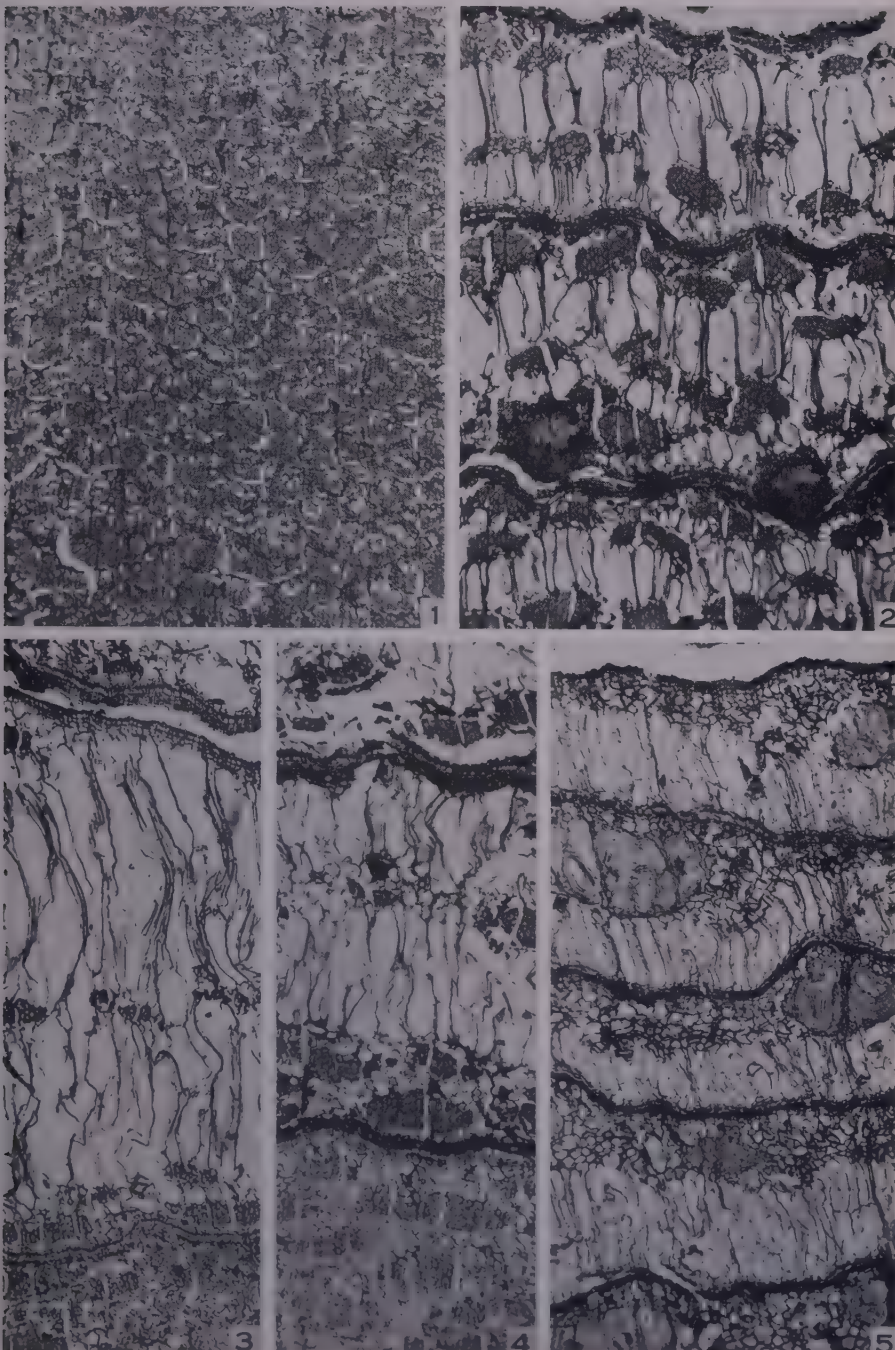
THE ANATOMY OF BARK. V



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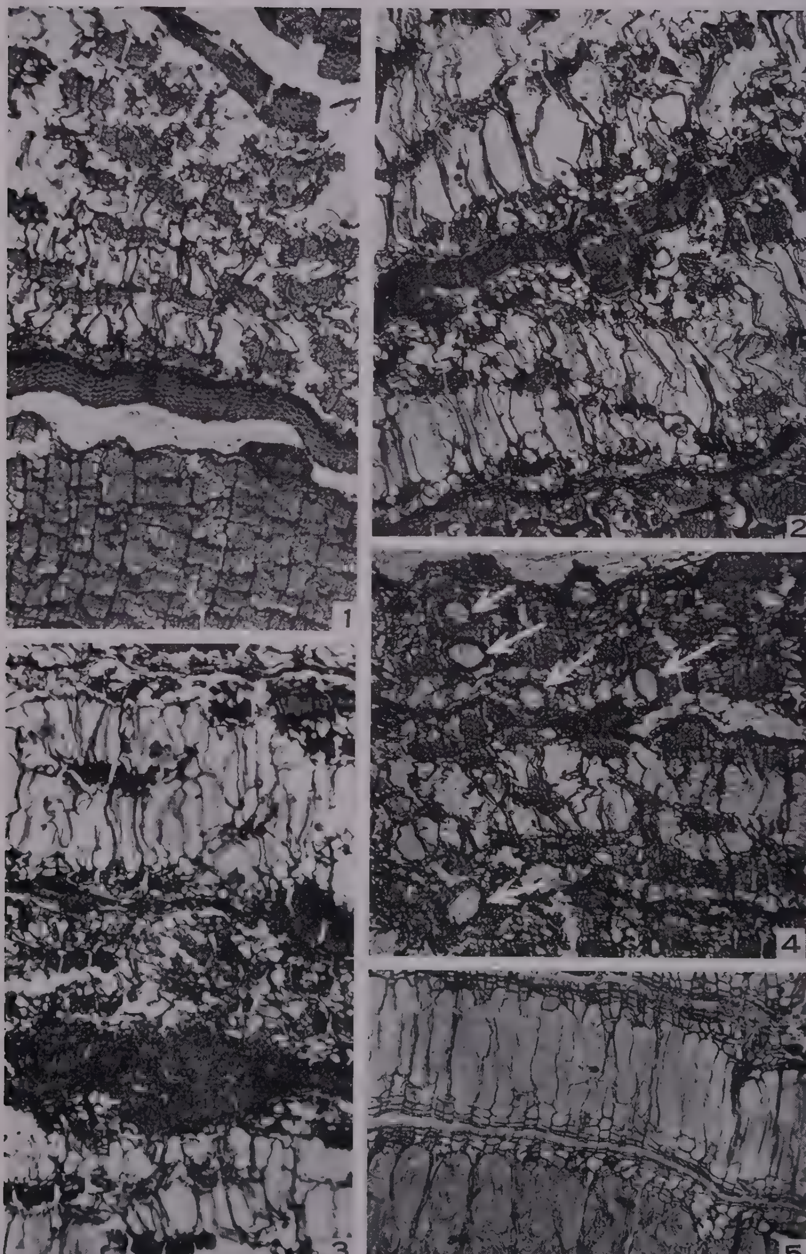

Explanation of Plates 1 and 2

Plate 1

Figs. 1 and 2.—*E. cameroni* Blakely & McKie. Cross sections of phloem (Fig. 1) and rhytidome (Fig. 2). × 40.

Figs. 3 and 4.—*E. microcorys* F. Muell. Cross sections of phloem and rhytidome to show variations in amount of parenchyma expansion. × 40.

Fig. 5.—*E. dichromophloia* F. Muell. Cross section of rhytidome. × 40.

Plate 2

Fig. 1.—*E. macrorrhyncha* F. Muell. Cross section of outer phloem and rhytidome, showing wide band of lignified phellem. × 40.

Fig. 2.—*E. wilkinsoniana* R. T. Bak. Cross section of outer phloem and rhytidome, showing wide band of lignified phellem. × 40.

Fig. 3.—*E. laevopinea* R. T. Bak. Cross section of rhytidome, showing variations in amount of parenchyma expansion. × 40.

Fig. 4.—*E. cinerea* F. Muell. Oil glands (at arrow), and expanded rhytidome parenchyma. × 40.

Fig. 5.—*E. setosa* Schau. Expanded rhytidome parenchyma. × 65.

THE ANATOMY OF BARK

VI. PEPPERMINTS, BOXES, IRONBARKS, AND OTHER EUCALYPTS WITH CRACKED AND FURROWED BARKS

By M. MARGARET CHATTAWAY*

[*Manuscript received January* 18, 1955]

Summary

The furrowed barks of peppermints, boxes, and ironbarks are due to cracks which extend through the rhytidome to the outermost phloem. In peppermints and boxes the cracks, which extend into the outer layers of the phloem, originate in the wedges of parenchyma that develop towards the periphery of the living phloem.

In the peppermints the furrows are schizogenous in origin. In the boxes they are more often lysigenous, the direction of the crack being often determined by the lysigenous kino pockets that form in the outer phloem. In the ironbarks they are lysigenous, the cell breakdown occurring most often in the inner layers of the wide rhytidome and only occasionally in the outer phloem.

Much of the width of rhytidome observed in many boxes and ironbarks is due to a wide phellem; their hardness is due to kino which occurs either as cellular kino or as large pockets formed by the breaking down of tissues of the outer phloem.

I. INTRODUCTION

In a general survey of the bark of the genus *Eucalyptus* (Chattaway 1953) a number of species which had "conspicuous parenchyma wedges" in the outer phloem were listed. These wedges were considered to be a method of increasing the perimeter of the tree trunk to accommodate the new growth of phloem and xylem added year by year as a result of cambial activity, but were not studied in relation to the formation of rhytidome. No attempt was made at that time to distinguish between the different tree groups, or to separate wedges which depend on contents or the development of stone cells to render them conspicuous, from those which are conspicuous solely on account of size.

Recently *Eucalyptus* species with oil glands in the phloem were described (Chattaway 1955*a*); in many of these the oil glands occur in close connexion with the parenchyma wedges of the outer phloem, and are formed as a result of a breakdown of some of the cells of the phloem, and more rarely of the rays. Such species form in the main a closely related group.

The present paper deals only with the rough-barked species, in which the successive layers of rhytidome are retained, becoming furrowed and cracked as they get older. In some of these, notably the peppermints and boxes, the furrows in the outer rhytidome originate from cracks in the parenchyma wedges of the outer phloem. The ironbarks owe their furrowed bark to cracks in the rhytidome, which seldom extend into the phloem. The phellem development is often much greater than in the boxes, and kino pockets form quite deep in the outer phloem.

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II. Material

The following species were available for examination. The classification is according to Blakely (1934) and the numbers in brackets indicate the number of samples available.

Peppermints

PIPERITALES: *E. andrewsii* Maid. (3); *E. campanulata* R. T. Bak. (7); *E. coccifera* Hook. f. (2)*; *E. dives* Schau. (13); *E. lindleyana* DC. (6); *E. linearis* Dehn. (2)*; *E. piperita* Sm. (5); *E. radiata* Sieb. (28) (including *E. australiana* R. T. Bak. & Smith); *E. risdoni* Hook. f. (2)*; *E. robertsoni* Blakely (8); *E. salicifolia* (Sol.) Cav. (3); *E. tasmanica* (Blakely) (2); *E. urceolaris* Maid. & Blakely (2). Five species were not available for examination.

Boxes

BUXEALES: *E. albens* Miq. (9); *E. behriana* F. Muell. (4); *E. bicolor* A. Cunn. (7); *E. boormani* Deane & Maid. (1); *E. bosistoana* F. Muell. (8); *E. brownii* Maid. & Cambage (1); *E. hemiphloia* F. Muell. (9); *E. hillii* Maid. (2); *E. leptophleba* F. Muell. (4); *E. microcarpa* Maid. (5); *E. microtheca* F. Muell. (5); *E. normantonesis* Maid. & Cambage (2); *E. pilligaensis* Maid. (1); *E. populifolia* Hook. f. (8); *E. rummeryi* Maid. (1); *E. tectifera* F. Muell. (2). Fourteen species were not available for examination.

Ironbarks

SIDEROPHLOIAE: *E. crebra* F. Muell. (1); *E. drepanophylla* F. Muell. (3); *E. jenseni* Maid. (1); *E. jugalis* Naud. (1); *E. leucoxylon* F. Muell. (8)†; *E. melanophloia* F. Muell. (6); *E. paniculata* Sm. (6); *E. pruinosa* Schau. (1); *E. siderophloia* Benth. (6); *E. sideroxylon* (A. Cunn.) Benth. (9). Seventeen species were not available for examination.

Other Species with Furrowed Rhytidomes

FRAXINALES: *E. sieberiana* F. Muell. (15); *E. consideniana* Maid. (5); *E. fraxinoides* Deane & Maid. (1). Twelve species were not available for examination.

PANICULATAE: *E. argillacea* W. V. Fitzg. (1); *E. howittiana* F. Muell. (1); *E. shirleyi* Maid. (3). One species was not available for examination.

SUB-BUXEALES: *E. blackburniana* Maid. (1); *E. calcicultrix* Maid. (1); *E. fruticetorum* F. Muell. (4)‡; *E. landsdowneana* F. Muell. & J. E. Brown (1)‡; *E. odorata* Behr & Schlecht. (2); *E. viridis* R. T. Bak. (7)‡. Seven species were not available for examination.

MELLIODORAE: *E. melliodora* A. Cunn. (26). This may vary from rough-barked to almost a smooth-barked species.

HETEROPHLOIAE: *E. baueriana* F. Muell. (3); *E. conica* Deane & Maid. (1); *E. fasciculosa* F. Muell. (1); *E. polyanthemos* Schau. (20); *E. rudderi* Maid. (1). Two species were not available for examination.

* Of the Piperitales, *E. coccifera*, *linearis*, and *risdoni* have a deciduous bark.

† Of the Siderophloiae, *E. leucoxylon* has a deciduous bark.

‡ Of the Sub-buxeales, *E. fruticetorum*, *lansdowneana*, and *viridis* are deciduous or very slightly rough at the base.

III. General Observations

(a) *Peppermints*

The peppermints have a rather soft, furrowed bark, easily pulled from the tree and always much decayed towards the periphery. It contains little tannin beyond what is normally present in the outer phloem. Sections of peppermint bark usually show a much decayed rhytidome in which fibres and parenchyma cells are almost completely disintegrated except on the edges of the furrows. Here the darker tissue contains heavier tannin deposits and proves more resistant to decay.

Fig. 1.—*E. robertsoni* Blakely. Cross section of outer phloem, showing a parenchyma wedge with a schizogenous crack. Early stages of the crack show inside the newly formed periderm. × 350.

As the trees increase in girth, wedges of tissue, derived from divisions of the phloem parenchyma, arise at intervals around the periphery of the phloem (Chattaway 1953). These wedges increase by division of the innermost cells of the wedge, resulting in tangential files of cells which are in a meristematic, actively dividing condition in the middle of the wedge (Plate 1, Figs. 1 and 2). These cells are at first conspicuous only by reason of their thinner walls, but later the cells begin to separate and intercellular spaces, which are normally absent from the phloem, appear, enlarging and separating the cells till a conspicuous crack is found. In the peppermints this crack appears to be schizogenous in origin, the cells seldom being torn but separating along the intercellular layer, leaving whole cells on either side of the furrow (Fig. 1). These spaces may widen extensively as further periderms

form, the wedges extending further in from the periphery and the cracks forming the characteristic network of furrows on the bark.

In connexion with the formation of heartwood it was found that, under conditions which lead to its ultimate death, parenchymatous tissue may be stimulated both to growth and to the production of tannins and gums in excessive amounts (Chattaway 1949, 1952). In the present instance, kino excreted from the cells of the parenchyma wedge fills the intercellular spaces and renders the line of separation conspicuous (Plate 1, Figs. 3 and 4; Plate 2, Figs. 1 and 2).

(*b*) *Boxes*

In the boxes the development of the parenchyma wedges at the periphery of the phloem follows, in its early stages, the same course as in the peppermints. The cracks that arise in the boxes are, however, schizogenous only in their very early stages, heavy deposition of kino accompanying the later lysigenous stages (Plate 2, Fig. 3; Plate 3, Figs. 3 and 4). Large kino pockets may form at the same time in the outer phloem, either in connexion with this breakdown of the parenchyma cells or independently of it. These pockets are commonly surrounded by a meristematic layer. from which suberized and lignified phellem similar to that of a normal periderm is cut off.

The boxes usually develop a wide phellem consisting mainly of successive layers of thin-walled suberized cells. This may be contrasted with the equally wide stringybark phellem, which consists almost entirely of thick-walled lignified cells (Chattaway 1955*c*).

(*c*) *Ironbarks*

Ironbarks, like the boxes, have a wide, much furrowed rhytidome, often full of kino. They seldom, however, have any very conspicuous wedges of parenchyma in the living phloem. Periderms form in almost every line of parenchyma in the outer phloem, and remain active for a considerable time, cutting off many layers of thin-walled suberized phellem. The furrows that are so conspicuous a feature of old ironbarks develop in the rhytidome and can be seen, in relatively young stems, to follow lines of lysigenous dissolution of the phellem. The furrows are usually more widely spaced than in peppermints and boxes and are consequently much wider. This aspect of older stems is accentuated by the fact that the hard brittle kino deposited throughout the rhytidome is very resistant to abrasion and consequently on an old ironbark the thick rhytidome may show cracks that are several inches wide at the surface of the bark. There is considerable variation in the amount of phellem produced, both between species and from sample to sample within a single species (Plate 4, Figs. 2 and 3). Sometimes the disintegration of the parenchyma results in a hard brittle bark full of kino pockets and cellular kino. Figure 2 shows the surface of a block of phloem and rhytidome of *E. paniculata*; the dotted lines represent successive periderms, the black areas kino pockets. At *b* and *d* the periderms have formed in close succession, at *c* there is an area where they are further apart.

In all the ironbarks examined the periderms were closer-spaced than in any other group of eucalypts. In some samples they form a fine anastomosing network. The texture of the resulting rhytidome depends on the amount of phellem that is produced. In some species only a small amount of suberized tissue is cut off and the resultant "cork" of the rhytidome is very hard, with many kino pockets; in others a very large amount of suberized phellem is produced by each phellogen, and the resultant "cork" is very spongy, even-textured, and waterproof. Such barks are shown in Plate 4, Figures 2 and 3.

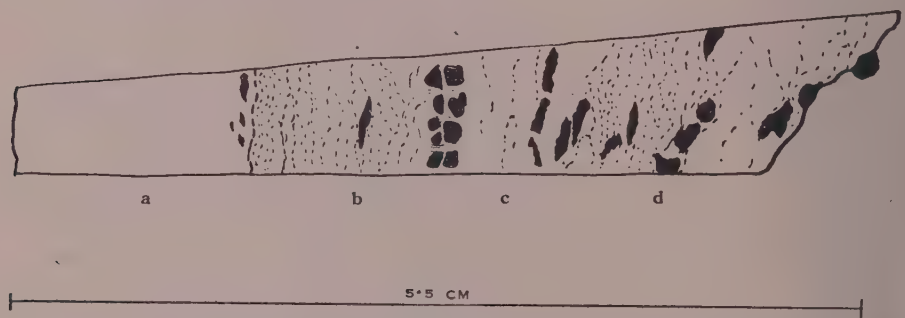

Fig. 2.—*E. paniculata* Sm. Cross surface of block of ironbark phloem and rhytidome. *a*, Phloem; *b*, *d*, areas with very closely spaced periderms; *c*, area with few periderms.

The rhytidome of peppermints and some boxes tends to decay easily; other boxes and the ironbarks have rhytidomes that seem very resistant to decay, even when they have the softer, spongy texture. The hard boxes and ironbarks appear to be protected by the hard kino they contain; the soft ironbarks consist mainly of suberized tissue which waterproofs the rhytidome and protects it against the penetration of fungal mycelia.

(*d*) *Other Species with Furrowed Rhytidomes*

Of the other species with furrowed bark, two, *E. vitrea* and *E. melliodora* (Plate 2, Fig. 4), develop schizogenous cracks in the same way as do the peppermints.

In the Paniculatae, *E. argillaceae*, *howittiana*, and *shirleyi* resemble the ironbarks (Plate 4, Figs. 1 and 2) with wide phellems but not very conspicuous wedges. In the Heterophloiae, *E. baueriana*, *conica*, *fasciculosa*, and *rudderi* have a box-like structure with lysigenous cavities and cracks. *E. polyanthemos*, however, is a rather variable species, some samples showing the lysigenous cracks and wide phellem of the boxes, and others (about six out of the 20 samples) a much more peppermint-like structure. These samples were all from one area, and possibilities of hybridization cannot be ruled out.

Three species in the Fraxinales, *E. consideniana*, *fraxinoides* (base of tree), and *sieberiana*, have a box-like structure in the rhytidome, with cracks arising by a tissue breakdown in the parenchyma wedges. These species, however, produce wide phellem, not of suberized cells like the boxes but of thick-walled lignified cells like the stringybarks. This is of interest as *E. gigantea* Hook. f. and *E. plan-*

choniana F. Muell., which are also in this group, have a stringybark type of rhytidome (Chattaway 1955*b*).

Parenchyma wedges which are associated with oil glands occur in the secondary phloem of certain other eucalypts; these have already been described (Chattaway 1955*a*). The oil glands are formed by the breaking down of parenchyma cells in the parenchyma wedges of the outer phloem. These wedges are, except for the oil glands, identical with those at present under discussion and are commonly the point of inception of furrows similar to those observed in the peppermints.

IV. Conclusions

At first sight it appears that all these wedges are a result of tree growth, providing a mechanism whereby the tissue at the periphery of the phloem accommodates itself to the ever increasing girth of the tree, and are no more than an extension into the secondary phloem of the tangentially stretched cells that grow and divide in the cortex of the young, actively growing stem. On further consideration, however, it is apparent that the wedges are not universal throughout the genus *Eucalyptus* but occur in certain closely related series, and that these series are not the only ones that include large trees. In most of the large trees there is some sort of expansion at the periphery of the phloem, but not large wedges of the magnitude of those under consideration. Furthermore, in these other large trees the expansion arises as a result of swelling and enlargement of existing parenchymatous cells, and not through the development of new cells from an actively dividing meristem in the middle of the wedge. The outer phloem of the peppermints and boxes is more heavily lignified than that of the stringybarks, many of the parenchyma cells having undergone enlargement and having secondary walls of variable thickness. The ones that remain meristematic become the basis of the parenchyma wedges. In a large wedge such as the one shown in Plate 1, Figures 1 and 2, the outer cells are the only ones that show any birefringence under polarized light, the central ones being still thin-walled and without secondary thickening.

Parenchyma wedges are connected with a cracked and furrowed rhytidome but cannot be essential to its formation, as they are absent from the ironbarks, the series in which cracks and furrows reach their greatest size and depth. As with other phloem features such as oil glands, radially elongated phelloderm, large fibres, and the expanded rhytidome of the stringybarks, the parenchyma wedges can be described and recorded, but it is impossible satisfactorily to assign any function to them.

V. Acknowledgments

The author wishes to express her indebtedness to all who have assisted with this paper, especially those who have collected material and checked its authenticity.

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Explanation of Plates 1-4

Plate 1

E. robertsoni Blakely: outer phloem and rhytidome

Fig. 1.—Parenchyma wedge in outer rhytidome. × 40.

Fig. 2.—Details of meristematic area of a parenchyma wedge. × 125.

Fig. 3.—Parenchyma wedge, line of future separation. × 40.

Fig. 4.—Details of tannin deposition in intercellular spaces. × 125.

Plate 2

Fig. 1.—*E. dives* Schau.: parenchyma wedge in outer phloem, with incipient crack. × 40.

Fig. 2.—Details of preceding. × 125.

Fig. 3.—*E. hemiphloia* F. Muell. Tannin deposits in cells abutting on lysigenous crack. × 40.

Fig. 4.—*E. melliodora* A. Cunn. Schizogenous crack penetrating into outer phloem. × 40.

Plate 3

Fig. 1.—*E. polyanthemos* Schau. Incipient disintegration of cells of parenchyma wedge to form lysigenous crack. The cells indicated by arrows stain differently from the rest. × 40.

Fig. 2.—Details of preceding. × 125.

Fig. 3.—*E. bosistoana* F. Muell. Early stages in formation of lysigenous crack. × 40.

Fig. 4.—Details of preceding. × 125.

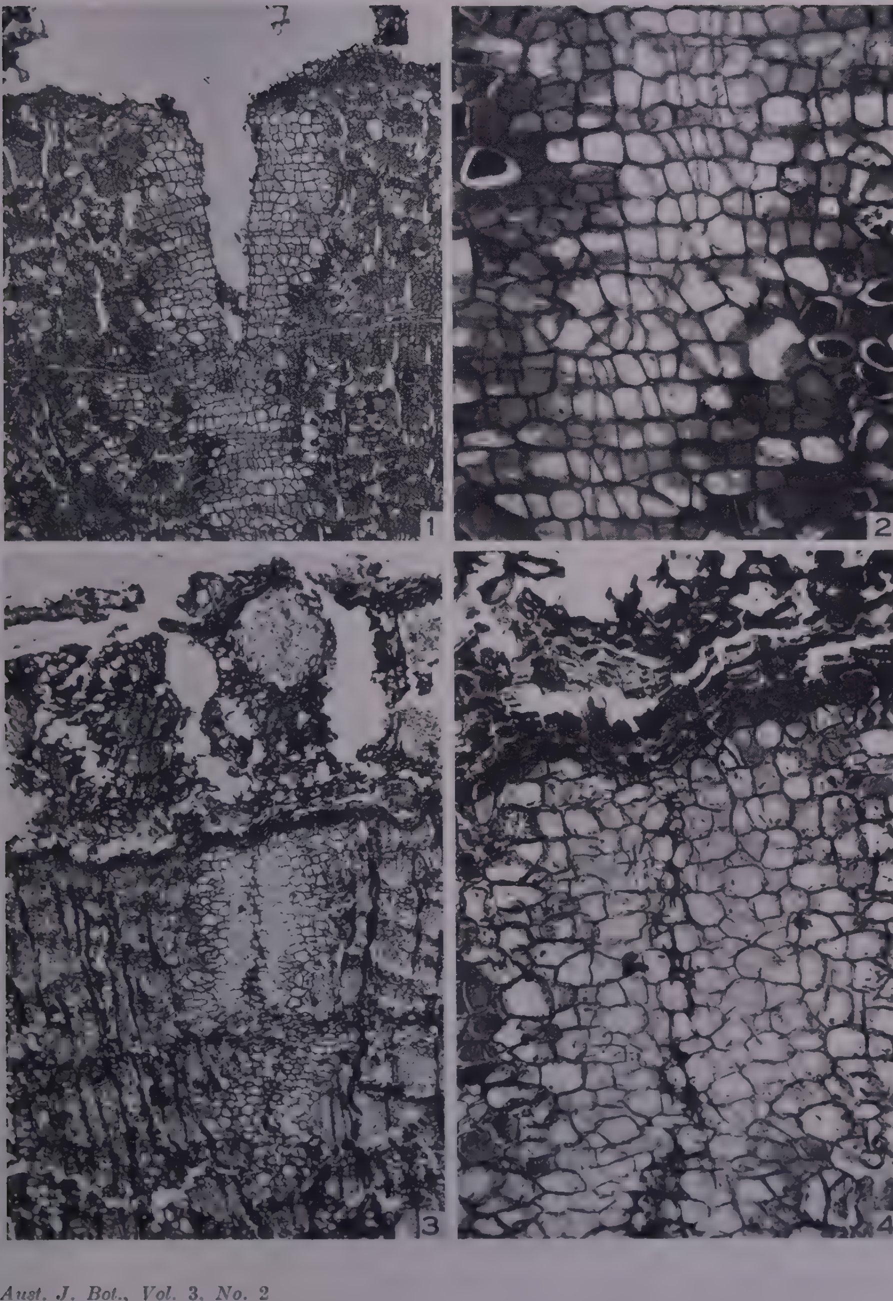
Plate 4

Fig. 1.—*E. shirleyi* Maid. Periderm formation in almost every parenchyma layer. × 125.

Fig. 2.—*E. crebra* F. Muell. Periderm formation in almost every parenchyma layer. × 125.

Fig. 3.—*E. drepanophylla* F. Muell. Outer rhytidome formed very largely of suberized phellem. × 27.

THE ANATOMY OF BARK. VI



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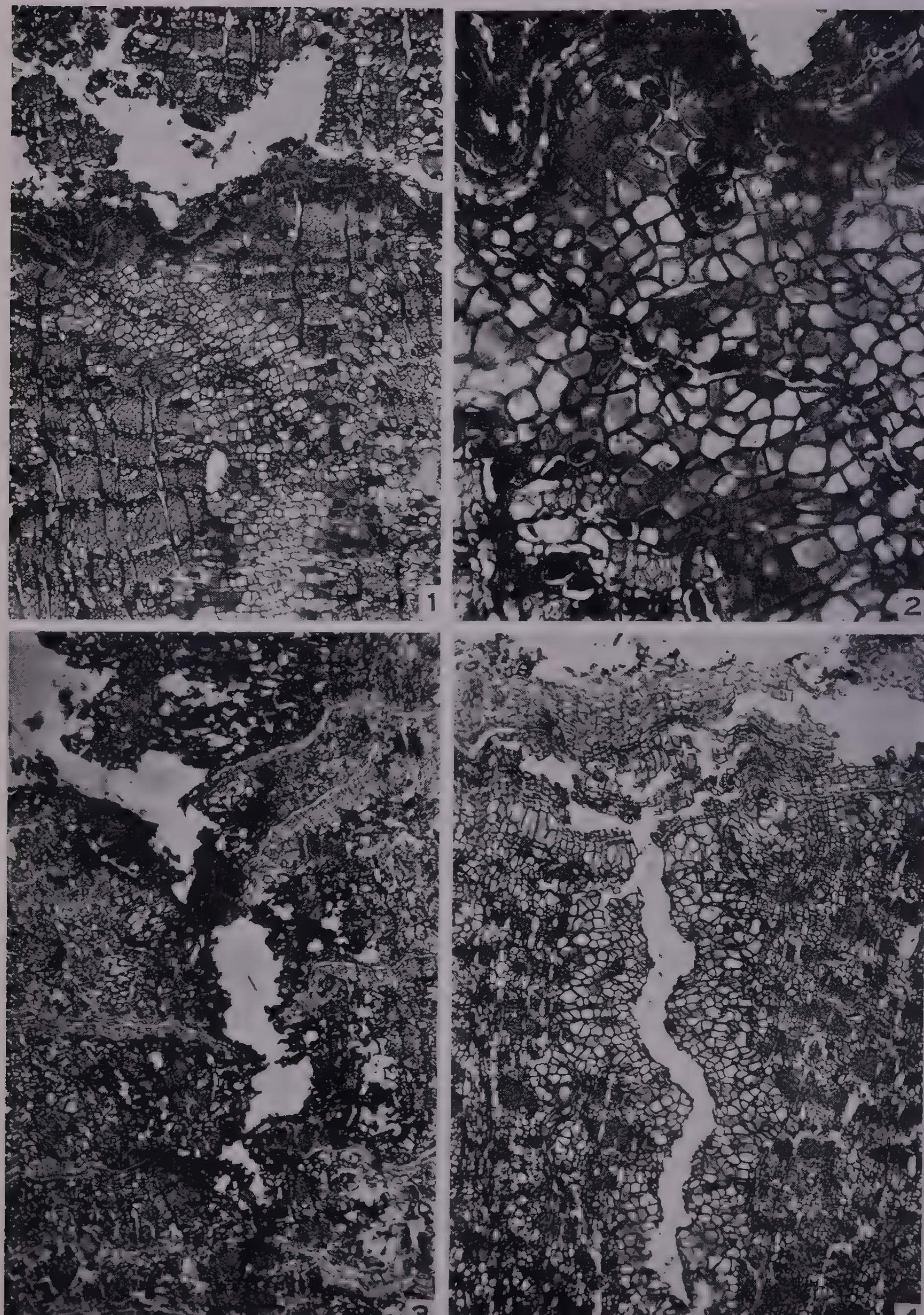

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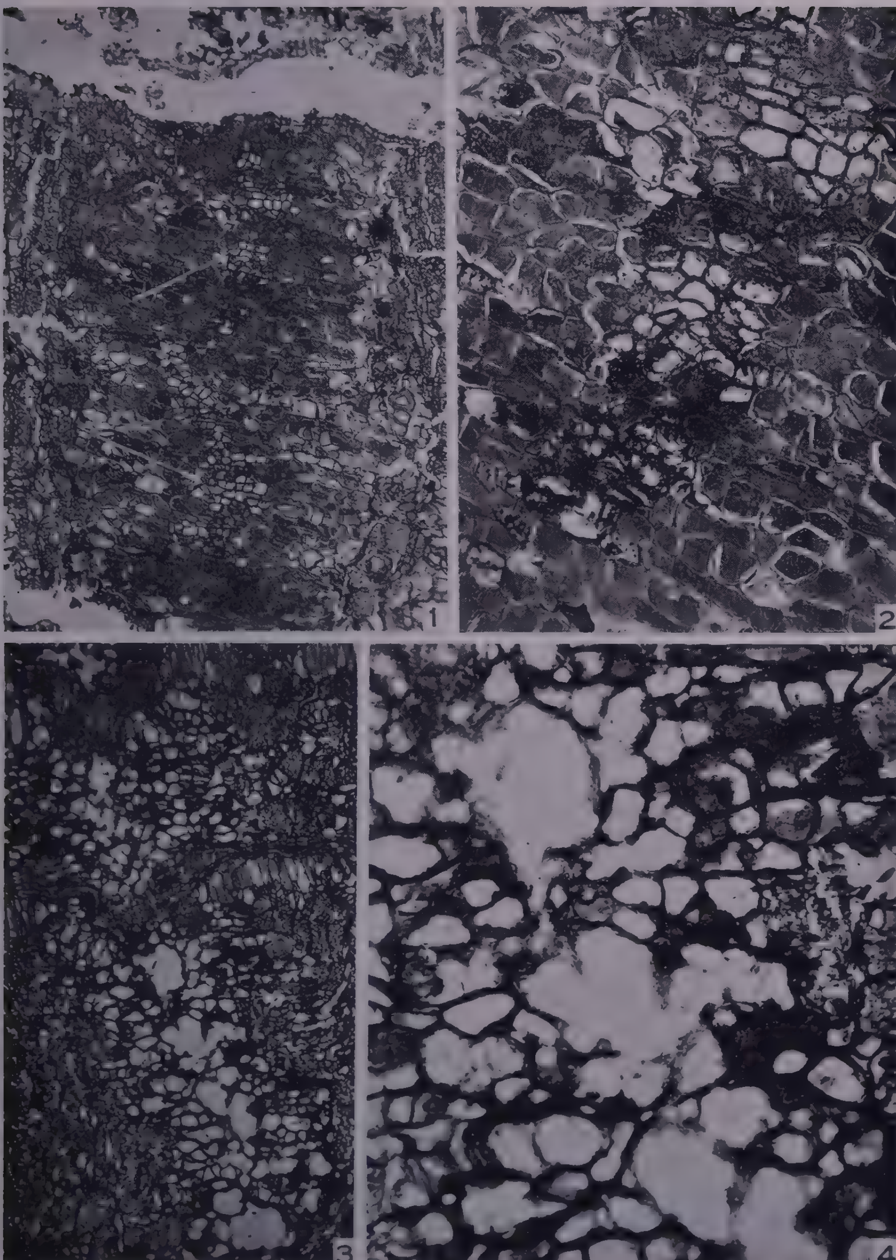

THE ANATOMY OF BARK. VI

THE NATURE OF REACTION WOOD

IV. VARIATIONS IN CELL WALL ORGANIZATION OF TENSION WOOD FIBRES

By A. B. WARDROP* and H. E. DADSWELL*

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Summary

The cell wall organization, the cell wall texture, and the degree of lignification of tension wood fibres have been investigated in a wide variety of temperate and tropical species. Following earlier work describing the cell wall structure of tension wood fibres, two additional types of cell wall organization have been observed. In one of these, the inner thick "gelatinous" layer which is typical of tension wood fibres exists in addition to the normal three-layered structure of the secondary wall; in the other only the outer layer of the secondary wall and the thick gelatinous layer are present. In all the tension wood examined the micellar orientation in the inner gelatinous layer has been shown to be nearly axial and the cellulose of this layer found to be in a highly crystalline state.

A general argument is presented as to the meaning of differences in the degree of crystallinity of cellulose. The high degree of crystallinity of cellulose in tension wood as compared with normal wood is attributed to a greater degree of lateral order in the crystalline regions of tension wood, whereas the paracrystalline phase is similar in both cases.

The degree of lignification in tension wood fibres has been shown to be extremely variable. However, where the degree of tension wood development is marked as revealed by the thickness of the gelatinous layer the lack of lignification is also most marked. Severity of tension wood formation and lack of lignification have also been correlated with the incidence of irreversible collapse in tension wood. Such collapse can occur even when no whole fibres are present, e.g. in thin cross sections.

Microscopic examination of collapsed samples of tension wood has led to the conclusion that the appearance of collapse in specimens containing tension wood can often be attributed in part to excessive shrinkage associated with the development of fissures between cells, although true collapse does also occur. Possible explanations of the irreversible shrinkage and collapse of tension wood fibres are advanced.

I. INTRODUCTION

In the first paper of this series (Wardrop and Dadswell 1948) evidence was presented that the secondary wall of tension wood fibres from *Eucalyptus regnans* F. Muell. was made up of three distinct layers, each of different micellar orientation. The orientations observed in the outer and middle layers were similar in arrangement to those of the same layers of normal wood fibres of the same species (Fig. 1(*a*)). However, the angle of orientation in the distinctive, broad, unlignified, inner so-called gelatinous or tertiary layer was approximately 5° with reference to the longitudinal fibre axis compared with the relatively large angle in the narrow, inconspicuous inner layer of normal wood fibres. This type of structure for tension wood fibres (see Fig. 1(*b*)) was considered to be the same for other species and appears to have been accepted by various workers, e.g. Freund (1951). However,

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additional work on tension wood in this laboratory has revealed that there may be several variations in the secondary wall structure and degree of lignification of tension wood fibres, both in the same species and in different species, depending on various factors of growth. Because tension wood occurs frequently in the timber derived from many species of commercial importance and because of its influence on the properties of such timber, a knowledge of the possible structural variations is considered of more than academic interest. Therefore, the structure of tension wood fibres from a variety of sources has been examined in some detail, and the results of this examination are presented here.

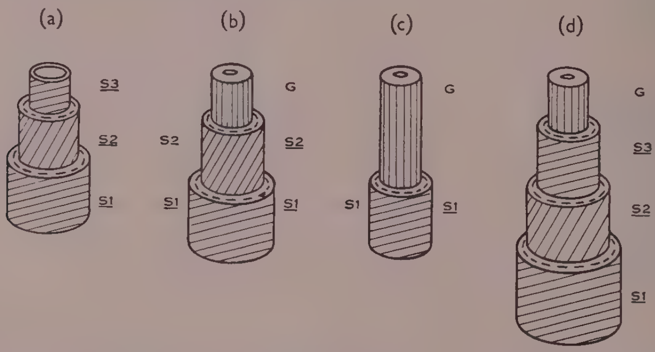

Fig. 1.—Diagrammatic representation of the organization of the secondary wall in (*a*) normal wood, and (*b*), (*c*), and (*d*) types of tension wood. *S*1 = outer layer, *S*2 = middle layer, *S*3 = inner layer, *G* = thick gelatinous (or tertiary) layer of tension wood fibre. Although the layer *S*1 is shown as having a single helical organization, in fact this may be a crossed structure. A bar under any of the above symbols indicates lignification of the layer concerned.

II. Material

Suitable specimens showing various stages of tension wood formation were obtained from locally grown species of the genus *Eucalyptus*, chiefly *E. regnans* F. Muell., *E. obliqua* L'Herit., *E. gigantea* Hook. f., *E. elaeophora* F. Muell., *E. goniocalyx* F. Muell. However, in addition, the tension wood in a wide range of material of both temperate and tropical regions was examined. This included the following species:

Acacia melanoxylon R.Br.
Artocarpus sp.
Barringtonia tetraptera Lauterb.
Casearia battiscombei R. E. Fries
Celtis leizonica Warburg
Celtis philippinensis Blanco
Emmenosperma alphitonioides F. Muell.
Evodia sp.
Fagus sylvatica L.
Ficus sp.
Garcinia sp.

Khava sp.
Kopsia sp.
Macaranga sp.
Myrtella sp.
Nothofagus cunninghamii (Hook. f.) Oerst.
Nothofagus grandis Steen.
Nothofagus menziesii (Hook. f.) Oerst.
Pimeleodendron sp.
Pipturus sp.
Pittosporum sp.
Populus sp.
Rhyticaryum sp.
Symplocos sp.
Xylosma sp.

and certain undetermined specimens of the Escalloniaceae, Euphorbiaceae, and Flacourtiaceae from New Guinea.

III. Experimental—Methods and Results

(*a*) *Investigations of Variations in Physical Organization*

(i) *Revealed by means of Polarization Optics.*—Cross sections (15-18 μ thick) of the various specimens showing evidence of tension wood were examined between crossed nicols. The ordinary fibres showed the normal three-layered structure, bright outer and inner layers separated by a dark middle layer (see Kerr and Bailey 1934). On the other hand, in most tension wood fibres under similar conditions only the outer layer appeared bright, the remainder of the cell wall being dark (see Plate 1, Figs. 1 and 2). This was the case for the various eucalypt species studied, as well as for most of the other species, but in some tension wood fibres of the undetermined new Guinea timber of the Flacourtiaceae the normal three-layered structure of the secondary wall was observed with, in addition, a dark, broad layer inside it (see Plate 1, Figs. 3 and 4). In all these cases the clearly distinguishable broad, unlignified, gelatinous or tertiary layer typical of tension wood was present.

Further, in closer examination of tension wood fibres in which, between crossed nicols, only the outer layer appeared bright, it was observed that three layers were not always present as previously described (Wardrop and Dadswell 1948, Fig. 1(*b*)). In these cases there was definite evidence of two layers only, namely, the outer layer and the gelatinous layer (Fig. 1(*c*)), e.g. in the early wood of *Eucalyptus gigantea*, in *Ficus* sp., and other specimens, in which the remainder of the cell wall within the bright outer layer appeared to be uniform and not composed of two distinct zones. This was confirmed by the examination of isolated single cell walls following the technique previously described (Wardrop and Dadswell 1948). It was interesting to note that the two-layered type of structure was present in the early wood in tension wood zones of one specimen of *E. gigantea* and the more common three-layered structure (Fig. 1(*b*)) in the late wood in the same specimen.

Besides the above variations in structure there appeared to be in any one specimen containing tension wood fibres a variation in the intensity of the develop-

ment of the layer G. Thus, in the sample of *Acacia melanoxylon* examined, one area from the edge of the tension wood band showed fibres in which a thin gelatinous layer was pulled away from the secondary wall (see Plate 2, Fig. 1). Another area in the middle of the band showed fibres with a thick gelatinous layer and little or no lumen (see Plate 2, Fig. 2). In the specimen of *Ficus*, three stages of tension wood formation were apparent. Between normal wood (A) (Fig. 1(a)) and what might be termed ordinary tension wood (C) (Fig. 1(c)), there was some intermediate tension wood (B) of similar organization to that shown in Figure 1(c), where the gelatinous layer G was not as well developed and the degree of lignification was much more marked. An additional stage of tension wood was, however, present. In this (D), the cells were completely unlignified, possessed a thick gelatinous layer G, and were considerably collapsed (see Plate 7, Fig. 1). In some samples tension wood fibres were also observed in groups mixed more or less indiscriminately with normal fibres as seen in Plate 2, Figures 3 and 4.

In all the specimens of tension wood examined, the major extinction position as determined from a single wall of a tension wood fibre prepared by the maceration of thin longitudinal sections was approximately axial. This is due to the influence of the thick gelatinous layer in which the micellar orientation must be practically parallel to the longitudinal cell axis.

(ii) *Revealed by X-ray Diffraction Methods.*—Using Cu Kα radiation and a specimen-film distance of 4 cm., X-ray diffraction diagrams were obtained for tension wood and adjacent normal wood from the following:

Barringtonia tetraptera Lauterb.
Emmenosperma alphitonioides F. Muell.
Eucalyptus regnans F. Muell.
Ficus sp.
Khaya sp.
Myrtella sp.
and the unknown Flacourtiaceae.

In general, the diagrams for tension wood were characterized by the small spread of the equatorial 002 arcs, the large number of spacings recorded, and the sharpness of the 021 arcs. These results were similar to those previously obtained with *Eucalyptus regnans* tension wood (Wardrop and Dadswell 1948). In the case of the specimen of *Ficus*, in which several degrees of development of tension wood were observed, a series of X-ray diagrams from normal wood (A) through to the extreme tension wood (D) was obtained. These are reproduced in Plate 3, Figures 1-4. Figure 1 may be regarded as typical of normal wood, and Figure 4 of definite tension wood, for all the material examined. In the various X-ray diagrams, arcs corresponding to spacings of 11 and 8 Å were observed in addition to the normal spacings of cellulose.

The X-ray diffraction diagrams for tension wood contained additional evidence for the existence of a well-developed cell wall layer with axial orientation of the crystallites. In comparison with diagrams from normal wood it can be noted that the diffraction arcs are sharper, indicating less angular dispersion of the diffracting regions about the longitudinal cell axis. In Plate 3, Figure 3, for example, the

dispersion is certainly less than 5°. However, long "tails" are apparent on the 002 diffraction arcs. The origin of these "tails" is not clear. Although it might well be argued that they are from the outer layer of the secondary wall, the theoretical analysis of Preston (1946) indicates that a flat helical orientation is manifest as a pair of equatorial arcs, whose density is greatest at their ends. This effect is apparent for the arcs of 5·4 and 6·1 Å spacing (e.g. Plate 3, Fig. 3), so that taking into account the diffuse scattering of non-crystalline constituents the low degree of dispersion of the 021 arcs reflects the almost axial orientation in the layer G. The X-ray diffraction diagram thus in effect corresponds to the superposition of a diagram of highly oriented cellulose arising from the layer G upon the diagram of considerably dispersed cellulose arising from the layer $S1$, or layers $S1$ and $S2$ (Fig. 1(b)).

(b) *Variation in Lignification of Tension Wood Fibres*

The degree of lignification in the cell walls of tension wood fibres was investigated by staining techniques and ultraviolet microscopy. As found previously (Wardrop and Dadswell 1948), by counterstaining cross sections with safranin and light green, the gelatinous or tertiary layer stained green in all cases. In the earlier paper it was stated that the remaining cell wall layers react with lignin stains such as safranin. However, in the present survey it was observed that the degree of lignification of tension wood fibres was variable, ranging from a condition in which the whole secondary wall was unlignified (green stain) to that in which the whole cell wall, with the exception of the gelatinous inner layer, was lignified (stained red). The variations observed are summarized in Figure 1, in which the underlining of the symbols for the various cell wall layers denotes lignification. In structural type "b" (see Fig. 1), layer $S1$ was always lignified, but layer $S2$ was sometimes unlignified. In structure "c", layer $S1$ was sometimes unlignified, but in structure "d" the three layers $S1$, $S2$, and $S3$ were lignified as in normal wood.

This staining technique has previously been shown (Dadswell and Ellis 1940) to give a reasonably reliable indication of the degree of lignification, and it has always given striking evidence of the presence of tension wood. Other staining methods for degree of lignification have been used, e.g. iodine followed by sulphuric acid, or the method of Coppick and Fowler (1939), but in all our recent work the safranin and light green double staining technique has been adopted as standard. Its value in this direction has been confirmed by parallel studies on certain specimens containing tension wood by means of ultraviolet microscopy. The lack of lignification in the gelatinous layers of tension wood fibres is shown by this method as can be seen for *Eucalyptus elaeophora* in Plate 4, Figures 1 and 2, and *Fagus sylvatica* in Plate 4, Figures 3 and 4. Lange (1950) has used this method in an attempt to determine quantitatively the amount of lignin in various parts of the cell wall of woody tissue. He, too, (Lange 1954) has demonstrated the absence of lignin in the layer G of the cell wall of tension wood fibres.

(c) *The Fine Structure of the Cell Wall*

Fragments from mechanically disintegrated tension wood fibres were mounted on grids, shadowed with uranium at an angle of 8°, and examined at a magnification

of 3000 in an R.C.A. type E.M.T. electron microscope. What was considered to be the gelatinous layer (*G* in Fig. 1) of the secondary wall in *Eucalyptus goniocalyx* is shown in Plate 4, Figure 5, and the outer layer in Plate 5.

In relation to considerations of the relative degrees of crystallinity, the density of cell wall substance was determined for both normal wood and tension wood of the same specimen. This was done using benzene as the displacement liquid at 29 °C, with the following results: normal wood 1·43 ,tension wood 1·47. It would appear that this difference is greater than would be expected from the difference in chemical composition (Cross and Bevan cellulose: normal wood 51 per cent., tension wood 65 per cent.). Also the equilibrium moisture contents of both normal and tension wood were determined over saturated potassium iodide solution at 20 °C. The results are set out in Table 1.

TABLE 1

EQUILIBRUIM MOISTURE CONTENTS OF TENSION WOOD AND NORMAL WOOD OF EUCALYPTUS REGNANS CONDITIONED OVER SATURATED POTASSIUM IODIDE SOLUTION AT 20 °C.

Specimen No.	From Green State*		From Oven-dry State†	
	Normal Wood	Tension Wood	Normal Wood	Tension Wood
1	17·51	16·38	13·10	12·67
2	17·43	16·45	13·51	12·62
3	17·33	16·50	13·25	12·68
Mean:	17·42	16·44	13·29	12·66

* By desorption from the green condition.

† By absorption after being oven-dried for 6 hr.

(*d*) *Investigation of the Anatomy of Collapse in Tension Wood Fibres*

One undesirable property of tension wood is its tendency to collapse in the very early stages of drying from the green condition; whereas collapse, when present in wood other than tension wood, usually responds normally to a reconditioning treatment, that in tension wood zones does not, even when the block of wood is boiled in water. Macroscopically this collapse sometimes appears similar to that occurring in normal wood (see Plate 6, Fig. 1), and microscopic examination of stained cross sections is often necessary to determine that tension wood is associated with the observed collapse. In other cases, the tension wood band can be readily recognized macroscopically both by its colour and the collapse that occurs. Such an example is shown in Plate 6, Figure 2, in which the tension wood present in the outer sapwood of a young stem of *Eucalyptus goniocalyx* shows severe collapse.

In the present investigation particular attention was paid to the anatomy of tension wood fibres in relation to the incidence of collapse and of internal stresses in the tension wood zones. It was observed that in some tension wood, as for example in one particular collapsed area of the specimen of *Ficus* (see Plate 7, Fig. 1), the appearance of the fibres in cross section was essentially similar to that in collapsed normal wood in which there is usually some considerable distortion of cell form. In species where the layer G is very thick, however, it appears that the macroscopic symptoms of collapse are due not only to collapse of individual cells but also to excessive shrinkage of the cell walls (see Plate 7, Fig. 2). Such shrinkage may or may not involve gross distortion of the tissue. In one experiment an oven-dried block of tension wood showing collapse was boiled in water before sectioning. It can be seen from Plate 7, Figure 2, that in this sample much irreversible shrinkage of the cell wall had taken place, often involving a permanent distortion of the cell wall (as at position marked B).

External collapse apparently depends on whether a sufficient number of adjacent cells undergo shrinkage or distortion and on the degree of cohesion between them. This can be seen in Plate 7, Figure 3, which is a photomicrograph of a cross section cut from a block of *Eucalyptus goniocalyx* tension wood, which, after drying, was embedded in a methyl and butyl methacrylate mixture (Newman, Borysko, and Swerdlow 1949) before sectioning, thus eliminating the possibility of recovery. Here, well-developed fissures (F) are apparent, gross distortion of the cells has taken place in regions around A, resulting in the complete collapse of a vessel V. In the lower right-hand corner of the photomicrograph the secondary wall does not show much distortion.

In a further experiment 18 μ cross sections were cut from fresh eucalypt tension wood and these sections oven-dried without restraint. The internal fissuring that developed is shown in Figure 4 of Plate 7.

IV. Discussion

(a) *Cell Wall Organization*

The generally accepted cell wall organization of normal wood fibres is shown in Figure 1(a) together with the 1948 proposal for the organization of tension wood fibres (Fig. 1(b)). In the present investigation it has been established that there are two additional possible structures for tension wood fibres, namely, those indicated in Figures 1(c) and (d). In one of these, "c", which type is fairly common in occurrence, only the outer layer $S1$ and the gelatinous layer G—typical of all tension wood fibres—are present. In the other, "d", which type is rare and was observed definitely only in some tension wood of the unknown specimen of the Flacourtiaceae, all three layers of the normal wood fibre are present, but there is the additional layer G. In all cases, the micellar orientation of the layer G is nearly parallel to the longitudinal fibre axis.

Onaka (1949) has referred to three types of gelatinous layer which may correspond to the three types of organization shown in Figure 1. However, he has indicated that each type is to be found in certain genera or families, whereas the present observations have demonstrated the occurrence of more than one type in a

particular specimen. Thus, in *Eucalyptus gigantea* type *b* was found in the late wood of one growth ring, and type *c* in the early wood of the following growth ring. A possible explanation, however, relates to the time in the growth cycle at which the stimulus responsible for tension wood formation is operative. The gelatinous layer which is the anatomical response to the stimulus may develop at different stages of secondary wall formation, depending on the rate of cell division and cell differentiation in the cambial zone at the time.

From the examination of X-ray patterns considerable information can also be obtained on the cell wall organization of tension wood fibres (see Preston and Ranganathan 1947; Wardrop and Dadswell 1948; Messeri 1953). In the present investigation the X-ray diffraction patterns obtained from tension wood were clearer, indicating less diffuse scattering of the X-rays and less angular dispersion, than in patterns from comparable normal wood. The type of pattern obtained corresponds to a nearly axial orientation of the cellulose micelles in the layer *G*.

From the results of the survey of the material used in the present study it would appear that there are degrees of lignification associated with tension wood development and further that the greater the development of the gelatinous layer the less the degree of lignification. In no case was there any evidence of lignification in the layer *G*, but in layers *S*1, *S*2, and *S*3 the amount of lignin present varied (Fig. 1).

(*b*) *Cell Wall Texture*

It was previously suggested (Wardrop and Dadswell 1948) that the degree of crystallinity of the cellulose in tension wood fibres was greater than in normal wood fibres. Further evidence of this was obtained in the present investigation. Thus, the lower equilibrium moisture content of tension wood (see Table 1), the higher density of the cell wall substance, and the sharpness of the X-ray diffraction diagrams are consistent with a high degree of crystallinity. However, the question arises as to the meaning of such a difference in terms of the submicroscopic texture of the cell wall.

It will be recalled that cellulose molecules in the cell wall are aggregated in crystalline regions, the micelles, which are detected by X-ray diffraction techniques. With the advent of the electron microscope, however, the cellulose was seen to be present as long threadlike aggregates called microfibrils. Some controversy has taken place as to the relation between the micelles and the microfibrils. It now seems clear that the microfibril is a super-micellar structure consisting of a number of micelles (Frey-Wyssling and Mühlethaler 1946; Wardrop 1949; and Frey-Wyssling 1954). It was suggested independently by Wardrop and Frey-Wyssling that each micelle is surrounded by a paracrystalline phase of cellulose molecules, i.e. molecules parallel with those in the micelles but lacking order in the two transverse directions. Wardrop (1949) also suggested that lignin and hemicelluloses, difficult to extract, are located between the molecules of this paracrystalline phase.

Frey-Wyssling (1954), on the basis of Vogel's (1953) experimental evidence, proposed that both the micelles and microfibrils are of laminar form so that the hydroxyl-rich 101 planes are parallel with the broad face of the microfibril which

is in turn parallel with the cell surface. Evidence for this proposed orientation of the 101 planes had been furnished by Sisson (1936) and Preston and Astbury (1937).

In interpreting the meaning of differences in the degree of crystallinity in terms of the above structure of the microfibril, Frey-Wyssling considered that such differences could be attributed to the amount of paracrystalline cellulose present. However, this view fails to take account of the known variation in different celluloses of the degree of lateral order of the micelles (see Wardrop 1954). If this is done, it is obvious that theoretically a difference in the degree of crystallinity may arise from:

(i) a difference in the amount of paracrysralline cellulose with micelle size (i.e. amount of crystalline cellulose) constant;
(ii) a difference in size of the micelle (extent of the region exhibiting lateral order) with the amount of paracrystalline cellulose constant; or
(iii) a difference both in the amount of paracrystalline cellulose and of micelle size.

TABLE 2

BREADTH AT HALF-MAXIMUM INTENSITY (RADIANS) OF THE 022 DIFFRACTION LINE OF NORMAL WOOD AND TENSION WOOD OF EUCALYPTUS GONIOCALYX

Specimen	Line Breadth	
	Untreated	Hydrolysed*
Normal wood	0·070	0·062
Normal holocellulose	0·059	0·052
Tension wood	0·049	0·046

* Hydrolysed with 8% hydrochloric acid for 15 min at 100 °C.

To assess which of these possibilities is applicable in any given case, it is necessary to be able to assess the micelle size, the amount of paracrystalline cellulose, and the degree of separation of the micelles within the microfibril. Absolute estimation of these quantities presents considerable difficulties but differences can be detected. Thus, some estimate of the micelle breadth as reflected in the degree of lateral order can be deduced from the line breadth in X-ray diffraction diagrams. It can be seen from Table 2 that the 002 diffraction line breadth is narrower in tension wood than in normal wood, indicating that the degree of lateral order is greater in the tension wood.

The estimation of the relative dimensions of the spaces separating the micelles in cellulose is difficult, as the methods used—such as measuring the size, from X-ray data, of metal crystals deposited in the intermicellar spaces—are open to the objection that such a deposition involves swelling of the cellulose (Frey-Wyssling

1937). In the samples of tension wood and normal wood examined by the writers the size of the gold crystals deposited showed no difference. This result, however, does not preclude that the spaces in the tertiary layer G may have been greater than in the other cell wall layers, because, if the layer $S1$ has a similar texture in both normal wood and tension wood, then the gold deposits in this layer would give broad lines in the X-ray diagram which would mask narrower lines arising from large deposits in other layers; but at least the evidence does show that the spaces in the layer G are no less than those in normal wood. Howsmon (1949) observed that on hydrolysis with dilute acid there was an increase in the apparent crystal size (Wardrop 1949; Foster and Wardrop 1951). This change could be explained on the assumption that the paracrystalline phase crystallized during hydrolysis. On the basis of such an interpretation differences in the extent of the paracrystalline phase should be manifest in different degrees of sharpening of the diffraction lines on hydrolysis. On calculating the apparent crystal size from the data in Table 2 it can be shown that under comparable conditions of hydrolysis the apparent crystal size of normal wood and that of tension wood increased to approximately the same extent, suggesting that the amount of paracrystalline cellulose was similar in the two cases. On this basis, therefore, any difference in the high degree of crystallinity is to be attributed to a greater micelle size in the tension wood, with a similar amount of paracrystalline cellulose to that in normal wood.

One further observation of general implication may be made. In measuring the change in apparent crystal size during hydrolysis, it can be seen from Table 2 that delignification of normal wood resulted in an increase in apparent crystal size. This result suggests that lignin is associated with the paracrystalline phase. It is thus reasonable to assume that the paracrystalline cellulose is present in the intermicellar regions and that some of the non-cellulosic constituents are associated with it.

Finally, it is not suggested that the micelles are of constant size—indeed, there is indirect evidence that a distribution of micelle size exists (Foster and Wardrop 1951). From these considerations the conclusion emerges that the microfibril, if we accept it as a biological unit, is composed of crystalline regions surrounded by a paracrystalline phase, so that its own surface is paracrystalline. The significance of the crystalline regions is difficult to assess, i.e. whether they are units of uniform size (Frey-Wyssling 1954), or whether they simply represent regions of irregular dimensions of more perfect molecular orientation within the microfibril and having no structural significance of their own. The latter view would appear the more probable.

(c) *Collapse in Tension Wood*

On the basis of the conventional theory regarding the cause of collapse in timber, no collapse would be expected when the thickness of the specimen was less than the average fibre length, and this was demonstrated by Greenhill (1936). In tension wood, however, considerable distortion of thin sections takes place on drying, involving changes in structure similar to those already observed in sections cut from collapsed blocks. Such observations are consistent with the view that

much of the distortion (collapse) which takes place in the drying of tension wood can be attributed to greater shrinkage of the cell wall.

For an explanation of the severity of collapse in tension wood the operation of several factors may be important. In the first place it will be clear from Figures 3 and 4 of Plate 7 that in tension wood collapse and transverse shrinkage are frequently associated with the development of fissures between the cells so that the continuity of the tissue is to some extent interrupted and shrinkage can proceed without the development of very great drying stresses. By contrast, in normal wood the cohesion of the collapsed tissue would be expected to involve the development of considerable stresses. In the second place, it is possible that a feature of cell wall organization or of cell wall texture may be involved in the irreversibility of changes that appear to take place in the drying of tension wood. The one major difference between normal wood and tension wood cell wall organization is the replacement of the layer *S*3, of flat helical orientation in the normal wood fibre, by the unlignified tertiary layer *G*, oriented axially in the tension wood fibre. The lumen diameter changes very little during the swelling and shrinkage of the normal fibre (see Stamm 1944). Now the cell wall can shrink by about 15-30 per cent. in normal wood (Roth 1894), and as this is very much greater than the external shrinkage of the block it is obvious that very considerable stresses must be set up in the fibre walls during drying. That this is so is, of course, well known. It is reasonable to suppose that during drying the layer *S*3 in the fibre tends to prevent the inward collapse of the cell wall. In the absence of layer *S*3, as in tension wood, and with the great shrinkage of the layer *G*, the whole fibre will be deformed during drying if the cohesion between the cell wall layers is as great as within them; on the other hand, no deformation of the fibres will take place if the layers separate during drying. Observations made support this interpretation.

Even if the layer *G* is accepted as the source of high shrinkage the irreversibility of such shrinkage remains to be explained. One possibility is that the lack of lignification in tension wood permits the development of "junction points" between the micelles of microfibrils—perhaps by hydrogen bonding—and these are not destroyed on re-swelling. However, if increased hydrogen bonding occurs in tension wood during drying, the difference in equilibrium moisture content by desorption and absorption should be greater than in normal wood. From Table 1 it is clear that this is not so; indeed the difference is greater in normal wood than in tension wood. Therefore, it is considered that this cannot be the explanation although it is recognized that the results quoted in Table 1 may not be strictly comparable (i) because of the greater degree of lateral order of the crystalline regions of tension wood in which relatively fewer hydrogen bonds could effect the same degree of irreversibility, and (ii) because the lack of lignification in tension wood which might influence the values, irrespective of hydrogen bonding which may occur.

In general, lignified tissues are more elastic than unlignified ones; thus, cotton fibres, which are unlignified, have a circular cross section when taken from the cotton boll, but collapse irreversibly on drying to a ribbon-like shape. On the other hand, the cells of the annulus of ferns are lignified and collapse on drying

but recover when the water column within them is ruptured during spore dispersal. These examples may be considered broadly analagous to collapse in tension wood and normal wood. The difference in behaviour may be better understood if lignification is regarded as an impregnation of the cellulose structure—which is suggested by the observed swelling of cell walls undergoing lignification—so that the lignin acts as a reinforcement for the cellulose frame.

However, in spite of the various factors considered above, no completely satisfactory explanation has been reached as to the cause of the irreversible shrinkage of layer *G*.

V. Acknowledgments

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Explanation of Plates 1-7

Plate 1

Fig. 1.—Transverse section of *Eucalyptus goniocalyx* F. Muell., tension wood, ordinary illumination. × 1000. Note thick gelatinous layer. The structure of these cells corresponds to that shown in text Figure 1(*c*).

THE NATURE OF REACTION WOOD. IV

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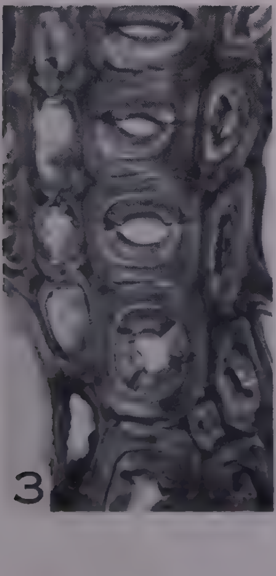

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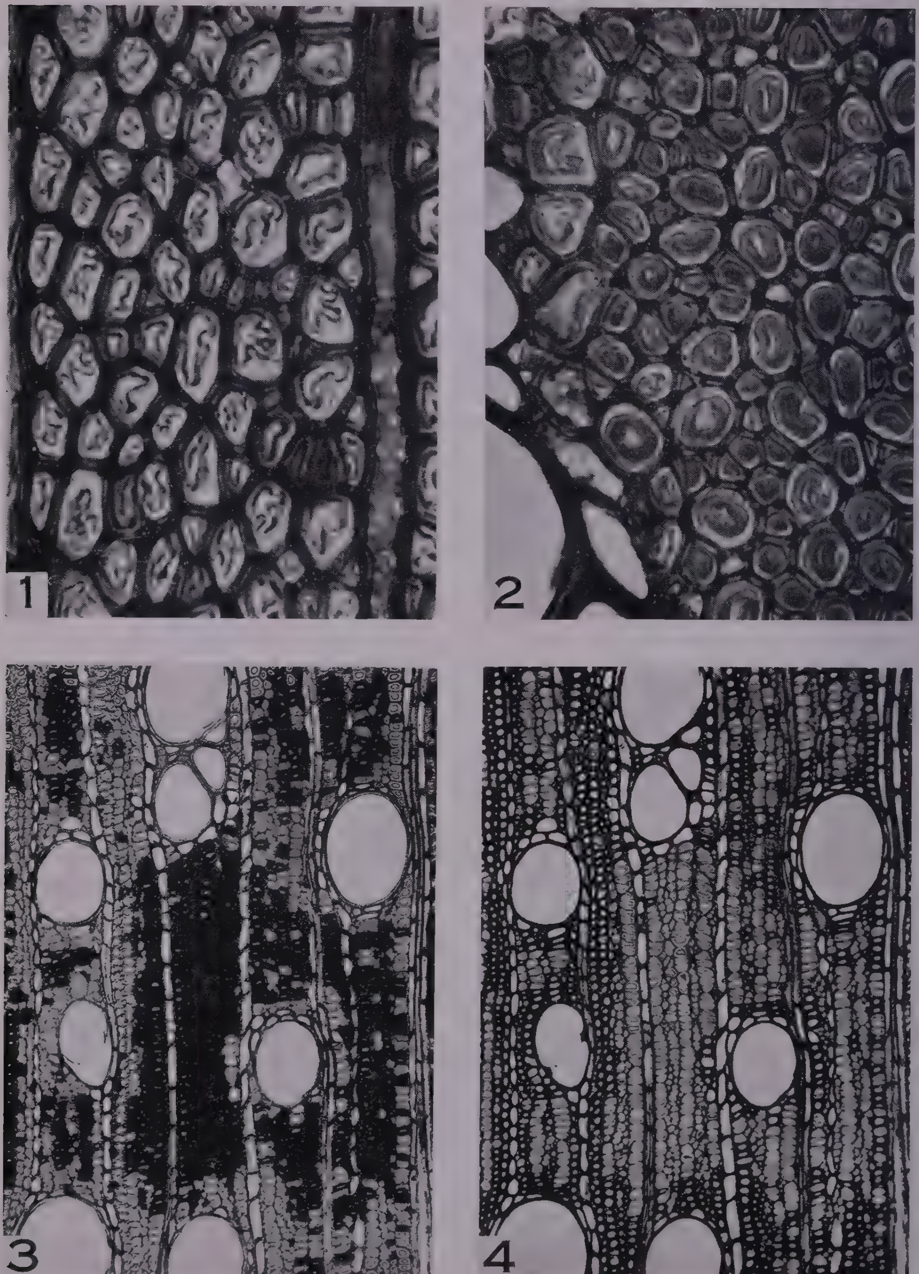
THE NATURE OF REACTION WOOD. IV



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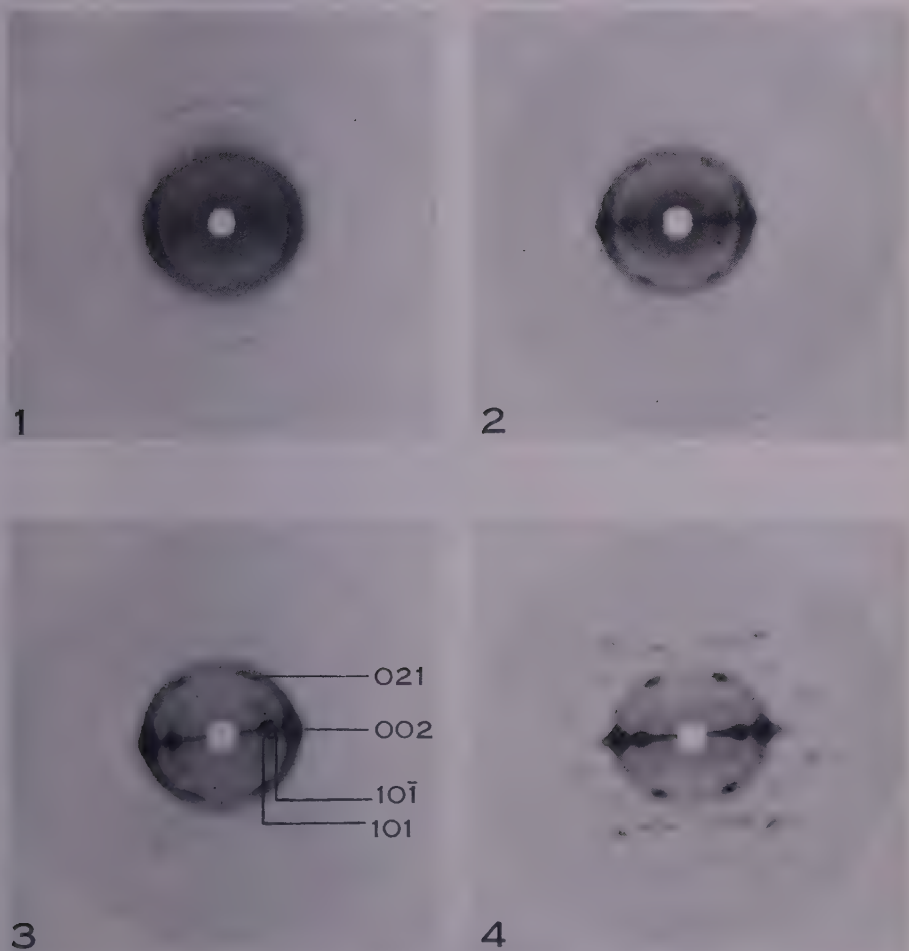

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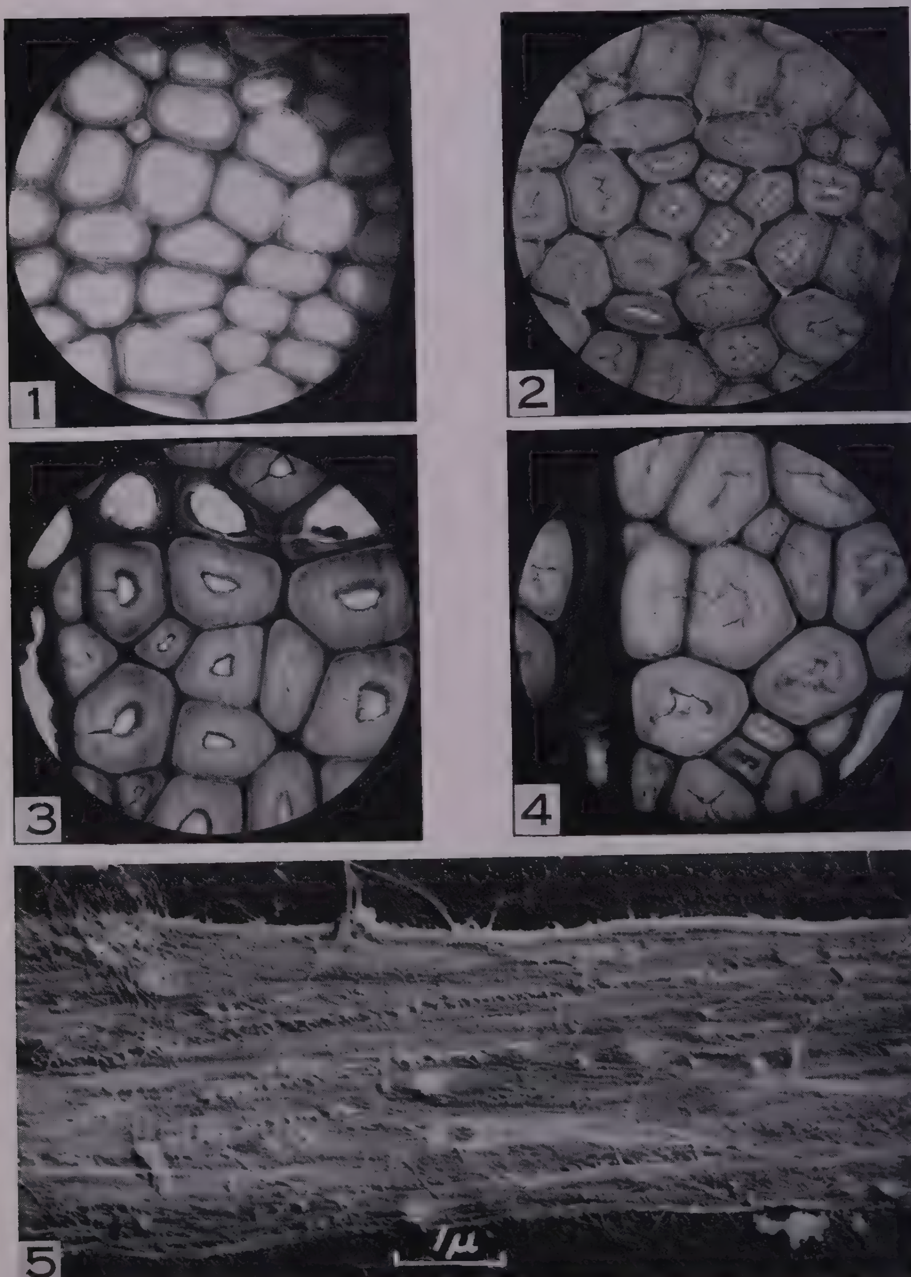

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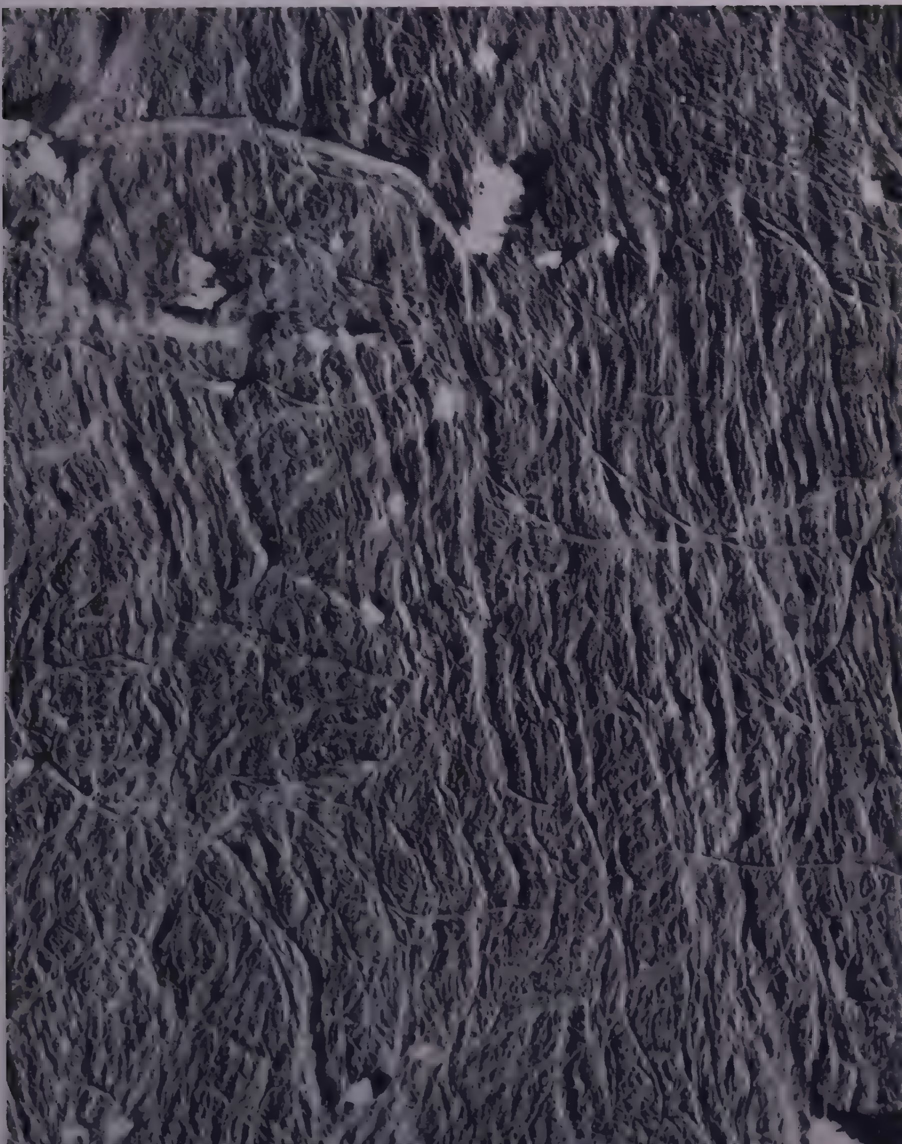

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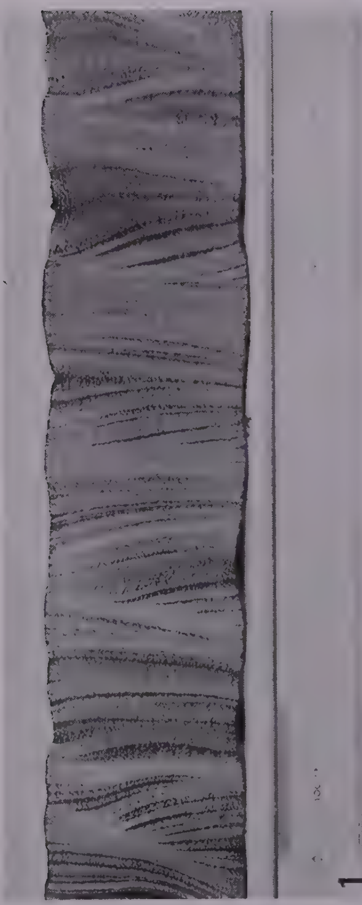

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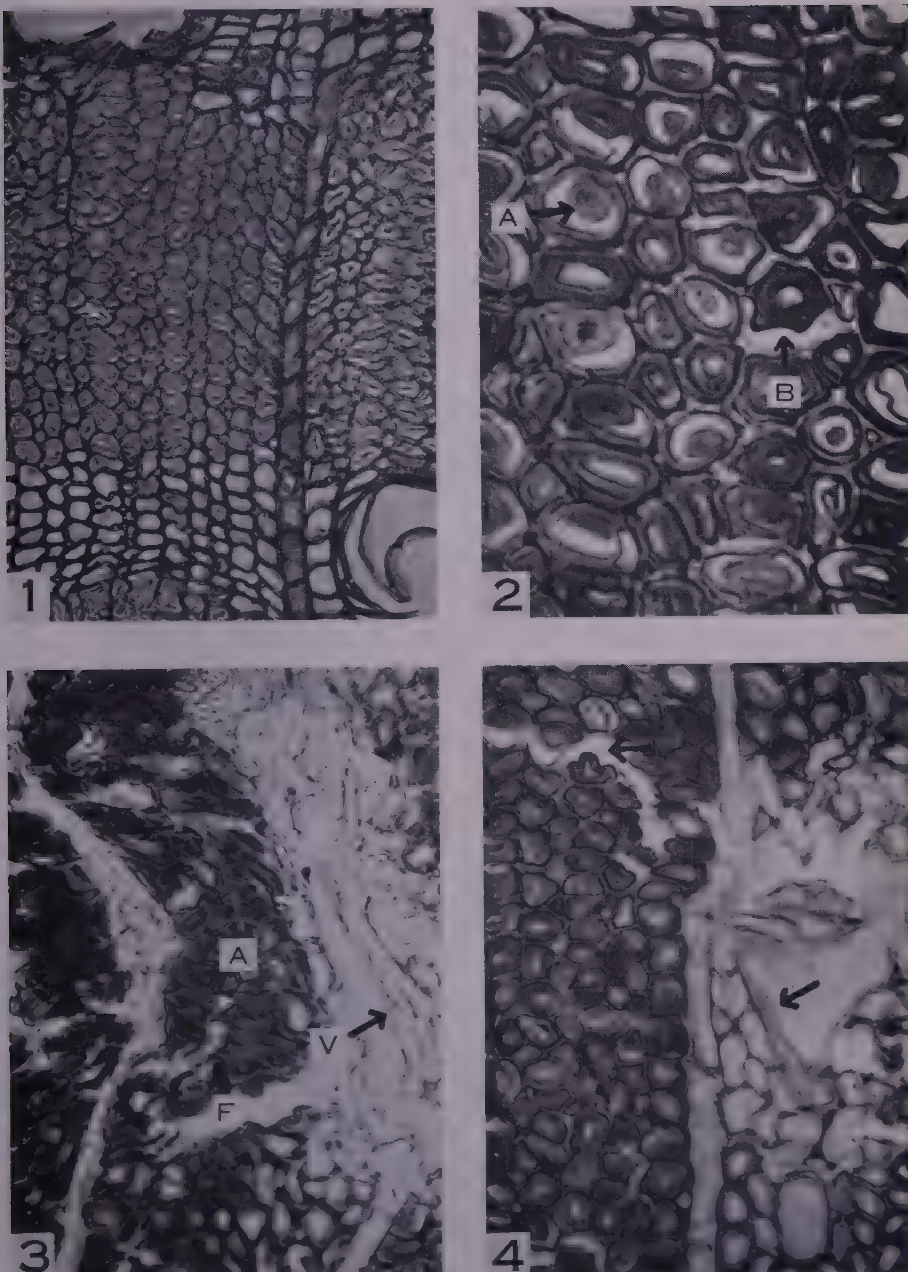

Fig. 2.—As in Figure 1, but photographed between crossed nicols. × 1000. Note that, apart from some halation near the centre, only the outer layer $S1$ appears bright.

Fig. 3.—Transverse section of tension wood from the undetermined specimen of the Flacourtiaceae from New Guinea. × 1000. Note layering in the secondary wall of the tension wood fibres; the organization of these fibres corresponds to that shown in text Figure 1(*d*).

Fig. 4.—As in Figure 3 but photographed between crossed nicols. × 1000. Note that both the outer layer $S1$ and inner layer $S3$ appear bright.

Plate 2

Figs. 1 and 2.—Transverse sections of tension wood in *Acacia melanoxylon*. × 400. Note variation in degree of development of layer *G*.

Figs. 3 and 4.—Transverse sections of tension wood in *Emmenosperma alphitonioides*. × 100. Note distribution of tension wood fibres in irregular groups. Figure 3 taken with red filter and Figure 4 same area with green filter.

Plate 3

X-ray diffraction diagrams of normal wood of *Ficus* (Fig. 1) and tension wood (Figs. 2, 3, and 4) of a specimen of *Ficus*. Cu Kα radiation. Specimen film distance 4 cm. Figures 2, 3, and 4 correspond to (B), (C), (D) types of tension wood described in text. The diffraction arcs 002, 10$\bar{1}$, and 101, correspond to the planes of 3·9, 5·4, and 6·1 Å spacing respectively.

Plate 4

Figs. 1-4.—Ultraviolet photomicrographs. × 810. ($\lambda < 2536$ Å).

Fig. 1.—*E. elaeophora* normal wood.

Fig. 2.—*E. elaeophora* tension wood.

Fig. 3.—*Fagus sylvatica* normal wood.

Fig. 4.—*F. sylvatica* tension wood.

Fig. 5.—Electron micrograph of part of the gelatinous layer (*G*) of *E. goniocalyx*. × 15,000.

Plate 5

Electron micrograph of part of what may be layer $S1$ of a tension wood fibre type (*c*), text Figure 1 (*E. regnans*). × 19,000.

Plate 6

Fig. 1.—Collapsed eucalypt board, note corrugated surface (tension wood bands are present).

Fig. 2.—Piece of sapwood from *E. goniocalyx*. Note effect of band of tension wood on collapse and longitudinal shrinkage.

Plate 7

Fig. 1.—Cross section of collapsed tension wood (type D) from the specimen of *Ficus* referred to in text and in Plate 3. × 200.

Fig. 2.—Cross section of tension wood from *E. goniocalyx* cut from a block after collapse and section re-wetted. × 1000. Note: *A*, pulling away of layer *G* due to high shrinkage; *B*, distortion of the cell.

Fig. 3.—Cross section of collapsed tension wood of *E. goniocalyx* cut from block after collapse (the block was embedded in a methyl and butyl methacrylate mixture to prevent recovery, if any). × 430. *V* = vessel, *F* = fissure between cells, *A* = group of distorted cells.

Fig. 4.—Cross section (18 μ) of *E. goniocalyx* tension wood cut before drying and allowed to dry without restraint. × 430. This shows development of fissures and some cell distortion due to shrinkage.

A HYBRID SWARM IN *CASSIA*

By D. E. Symon*

[*Manuscript received November 29, 1954*]

Summary

Cassia specimens collected from a transect on a hillside near Alice Springs, central Australia, showed many intermediate characters, the distribution of which were very suggestive of a hybrid swarm between *C. desolata* F. Muell. var. *involucrata* J. M. Black and *C. artemisioides* Gaud. The specimens were examined for seven characters, and the results are presented.

A cline up the hill in leaflet numbers in the species *C. artemisioides* is recorded.

I. Introduction

Some species of the genus *Cassia* growing in Australia have long been considered taxonomically difficult, and amongst herbarium specimens intermediate types can be found. Bentham, in "Flora Australiensis", indicates F. Mueller's opinion as follows:

"F. Mueller is disposed to consider this (*C. phyllodinea* R. Br.) and the preceding phyllodineous species (*C. circinata* Benth.) together with the five following ones (*C. eremophila* A. Cunn., *C. artemisioides* Gaud., *C. sturtii* R. Br., *C. desolata* F. Muell., and *C. oligophylla* F. Muell.) as forms of one species, and it is true that we occasionally meet with specimens apparently connecting them, but so it is with the whole section (Psilorhegma) from *C. glauca* to *C. circinata* which we certainly would not be justified in uniting." Later botanists have found them just as difficult but to date no substantial revision has been made.

Increasing numbers of hybrids in natural plant populations are reported from overseas but published works in Australia have been virtually restricted to the genus *Eucalyptus*.

During a trip to central Australia the opportunity was taken to examine much *Cassia* material in the field, and repeated suggestions of hybrid swarms were found. Between Alice Springs and Hermannsburg, at Palm Valley, and between Granite Downs and Oodnadatta, populations including most of the above species were examined and sampled but only at Alice Springs was quantitative evidence obtained. In June 1953 a transect was taken through a shrubbery of *Cassia* species growing on a low rocky hill some 10-12 miles north of Alice Springs. A sample of the material to be discussed is shown in Plate 1, and in Figure 1 the distribution of the specimens on a profile of the hill is illustrated.

The principal species involved were *C. artemisioides* and *C. desolata* var. *involucrata*, and, whilst considerable variation exists amongst these *Cassias* as indicated above, they can usually be separated on the characters shown in Table 1.

C. artemisioides is widely spread in the drier areas of Australia whilst *C. desolata* var. *involucrata* is contained within this general area but is more restricted to the central regions.

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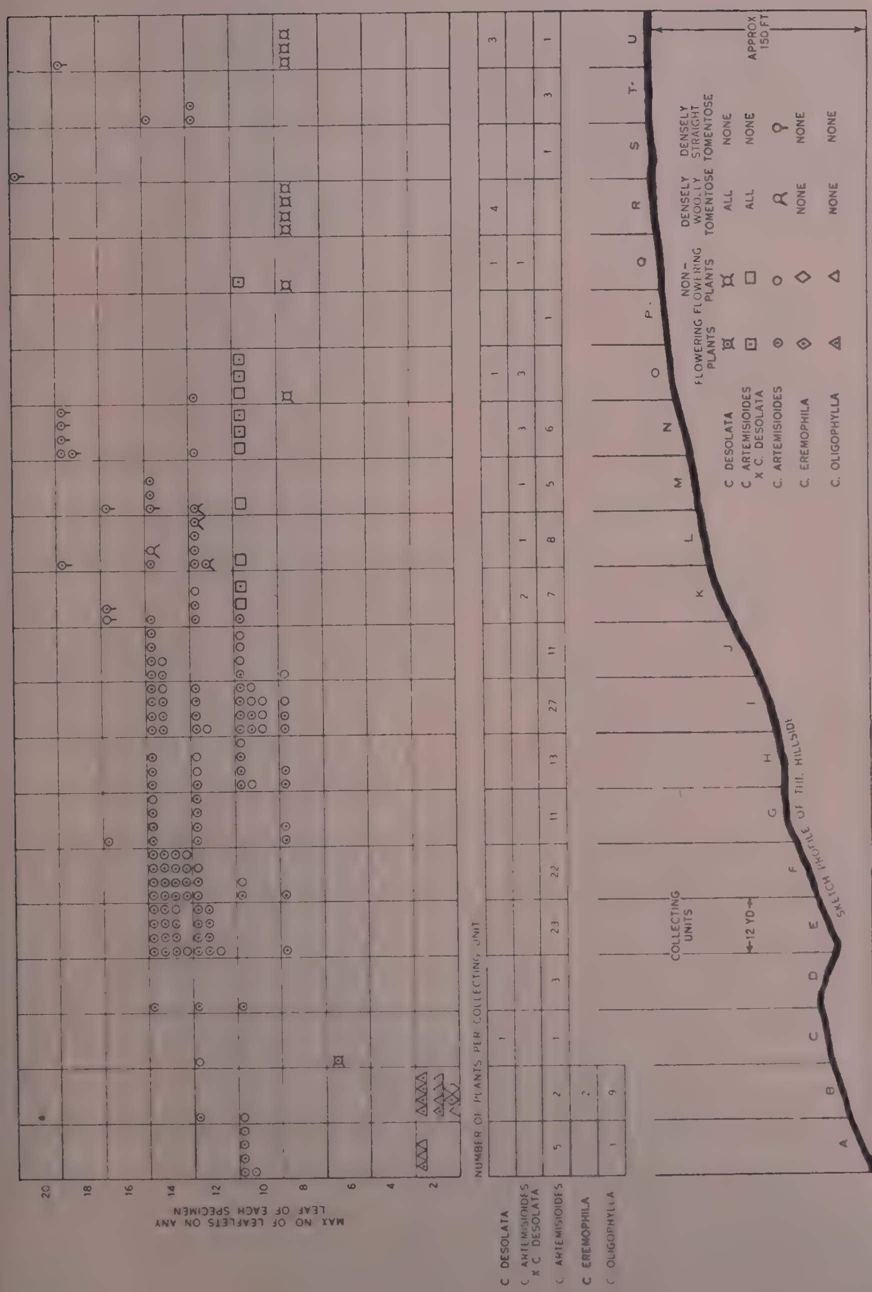

Fig. 1. - Sketch profile of the hill, showing the distribution and number of *Cassia* specimens and some of their characteristics.

II. Procedure

The transect, which consisted of a strip 10 paces (approx. 10 yd) wide by 250 paces (250 yd) long, was traversed from the base of the hill to its top. The collecting units were areas of 10 by 12 paces and within each a shoot was taken from every *Cassia* plant. Wherever the shrub was in flower a flowering shoot was selected. Seed pods were not common at the time and were not collected. The plant material was pressed and dried and has since been arranged in serial order. The soils were not examined in detail but were definitely skeletal on the two rocky outcrops and towards the top of the hill. The aspect was uniform and faced south-west whilst the elevation was between 100 and 150 ft above the plain.

Table 1

KEY TO SEPARATION OF CASSIA ARTEMISIOIDES FROM C. DESOLATA VAR. INVOLUCRATA

Characters	*C. artemisioides*	*C. desolata* var. *involucrata*
Plant	Shrub 3-8 ft	Shrub 3-4 ft
Leaflets	3-8 Pairs, terete single furrowed above, 6-40 mm long, 1-1½ mm dia.	3-4 Pairs, obovate, 1½-2 cm long, 1 cm wide
Tomentum	More or less hoary white with short appressed pubescence	Densely white tomentose with curly hairs
Glands	One between the lowest pair of leaflets	Usually one between each of the two lowest pairs of leaflets
Flowers	Yellow, in a short dense raceme	Yellow, 4-6 in an umbel
Pods	Thin, flat, 4-6 cm long, 8-10 mm wide	Thin, flat, obtuse, 4-7 cm long, 1½-2 cm wide

The material has been examined for the following characters: leaf size, the maximum number of leaflets per leaf and the pubescence upon them, the number of glands between the leaflets and their distribution. In addition the nature of the inflorescence, the time of flowering, and the apparent pollen fertility were examined. The physical distribution of the different species and their numbers as well as some of the characters mentioned above are shown in Figure 1.

III. Results

(a) Distribution

As can be seen from Figure 1, *C. desolata* was entirely restricted to the crest of the hill except for one plant collected on unit *C*. It was the only specimen of this species with six leaflets and in flower at that time.

The plants referable to *C. artemisioides* occurred over the whole area but were concentrated in the middle slope, areas *E* to *I* containing two-thirds of the total number.

In a zone between the main concentrations of *C. desolata* and *C. artemisioides* (areas *K*-*O*) was found a group of plants which were presumed to be hybrids between these two species on the basis of characters described below.

At the base of the hill and within the transect area were two plants only of *C. eremophila* and 12 plants of *C. oligophylla*.

TABLE 2

DISTRIBUTION OF MAXIMUM LEAFLET NUMBER ON 185 CASSIA SPECIMENS

Species	Maximum Number of Leaflets on any Leaf									
	2	4	6	8	10	12	14	16	18	20
C. desolata var. *involucrata*			1	9						
C. artemisioides × *desolata* var. *involucrata*					11					
C. artemisioides				10	30	40	58	4	7	1
C. eremophila	2									
C. oligophylla	12									

(*b*) *Number and Size of Leaflets*

The leaves of these *Cassias* are pinnate and consist of a number of pairs of opposite leaflets (Table 2; Fig. 1). Except for the specimen of *C. desolata* already mentioned, every sample of this species had a maximum of eight leaflets per leaf. Specimens of *C. artemisioides* had leaflet numbers ranging from 8 to 20 and all specimens of the suspected hybrids had a maximum of 10 leaflets on any leaf. It will be seen that the presumed hybrids are intermediate in this character between *C. desolata* and the bulk of *C. artemisioides*.

There was an increase in number of leaflets per leaf on *C. artemisioides* up the hill which was statistically significant at the 0·1 per cent. level of probability, and it formed a good example of a cline. All specimens of *C. eremophila* and *C. oligophylla* had one pair of leaflets only.

The leaflets of *C. desolata* are obovate and somewhat cuneate, those of *C. artemisioides* are (with a few exceptions to be mentioned later) terete. The intermediate plants have linear oblong leaves slightly tapered towards the base. Dimensions based on the dried plants are given in Table 3.

(c) *Tomentum*

Without exception the plants of *C. desolata* and the possible hybrids were covered with a dense woolly tomentum of irregular or curly hairs and there appeared to be little variation between specimens in this character. Nearly all the plants of *C. artemisioides* had a hoary pubescence with straight appressed hairs sometimes becoming almost glabrous with age. The density of these hairs varied both between plants and on the same plant. In the absence of a quantitative measure, data will not be given, but towards the base of the hill the plants more frequently become partly glabrous with age. In contrast, of the 33 *C. artemisioides* specimens

TABLE 3

LEAFLET DIMENSIONS OF THE CASSIA SPECIMENS

Species	Number of Plants	Length (mm)	Breadth (mm)
C. desolata var. *involucrata*	9	12 ± 1·3	6·4 ± 1·5
C. artemisioides × *desolata* var. *involucrata*	11	19 ± 2·7	3·9 ± 0·3
C. artemisioides	150	19·9 ± 3·4	1
C. eremophila	2	50	1
C. oligophylla	12	32·6 ± 2·5	10 ± 0·6

growing in collecting units *K* to *U*, four had an unquestionable dense, woolly, curly tomentum and in addition these four plants had a distinctively broader, deeper channel down the upper surface of the leaflets. Of the remainder, 11 had a dense woolly tomentum but with relatively straight hairs, and the rest had straight appressed hairs, all with normal terete leaflets. The appropriate plants are indicated in Figure 1 and, significantly, were in the region of the presumed hybrids. These were the only specimens which could be considered as possible backcross plants.

(d) *Glands*

The leaves of these species of *Cassia* usually have a gland between one or more pairs of the lower leaflets. Two leaves from every specimen were examined and scored for the number and position of these glands. They were not absent from any single plant, although an occasional leaf was found without glands, and some were apparently damaged by insects at an early stage of growth. Table 4 shows the gland frequency on the leaves scored from the 185 specimens. Again in this character the hybrid appears to be intermediate but does show a wider range than either postulated parent. The plants of *C. artemisioides* with leaves having higher numbers of glands are not noticeably concentrated in any area.

(e) *Flowering Times*

It is obvious that for any cross fertilization to occur the flowering times must at least overlap. It was found here, as had been noticed elsewhere, that *C. desolata* flowers later than *C. artemisioides* in the same locality. Only one *C. desolata* was in flower in the transect, although many were in an advanced bud stage and a few had begun to flower in nearby areas. In contrast to this, 80 per cent. of the *C. artemisioides* were in flower. It was therefore interesting to find that 6 of the 11 hybrids were in flower. Half of the *C. oligophylla* and *C. eremophila* plants were flowering.

Table 4

NUMBER OF GLANDS ON THE LEAVES OF THE CASSIA SPECIMENS

Species	Leaves Examined	Number of Glands per Leaf				
		0	1	2	3	4
C. desolata var. *involucrata*	20		5	13	1	1
C. artemisioides × *desolata* var. *involucrata*	22	1	13	3	3	2
C. artemisioides	301	23	245	24	9	
C. eremophila	4		4			
C. oligophylla	24	2	22			

(f) *Inflorescences*

The inflorescence of *C. desolata* is an umbel or a very compact raceme; that of the hybrid is a raceme, at times rather compact but looser than that of *C. desolata*. The inflorescence of *C. artemisioides* is a raceme, which may be loose (more commonly) or compact. Differences in the growth stages made detailed analysis difficult. In all cases the individual flowers were yellow and were subtended by deciduous bracts.

(g) *Pollen Fertility*

Where flowers were available counts were made of the stainable pollen on selected specimens using cotton blue in lactophenol as the stain. The sole flowering plant of *C. desolata* had 99 per cent. of stainable pollen and the values for the six presumed hybrids that were flowering were 89, 91, 94, 95, 95, and 97 per cent. Eight of the possible backcross types had values between 91 and 99 per cent. and six plants of *C. artemisioides* chosen at random had values between 87 and 97 per cent. These values suggest that infertility coming from sterile pollen is unlikely, and raises the question as to whether the presumed hybrids are truly so.

IV. Discussion

The presumed hybrids are very uniform morphologically (as is *C. desolata* in this collection) and they do not reflect the differences in leaf number shown by *C. artemisioides*, although the sample is not a large one. The possible backcross plants are all much closer to *C. artemisioides* than to *C. desolata*. However, owing to the sparser distribution of shrubs on the hilltop, the number of plants within the upper transect units is much fewer so that a small proportion of possible backcross types could readily have been missed. Their apparent absence could also be due to their being at some physiological disadvantage and their being eliminated by severe ecological selection occurring on this torrid site. Elsewhere, and amongst the great many herbarium specimens since examined, possible backcross types in the direction of *C. desolata* have been found. In the other areas mentioned earlier some apparently intermediate plants bore seed, and amongst the few seedlings grown to date there is no evidence of segregation for gross morphological characters.

The situation is extraordinarily like that discussed by Dobzhansky (1953)* when describing the occurrence of natural hybrids in *Arctostaphylos*. Here two ecologically separated species produced F_1 hybrids; backcross plants did occur but appeared rare. Natural selection apparently eliminated most or all recombination products, so that, despite the formation of viable and fertile hybrids and the maintenance of a narrow channel of gene exchange, the genetic systems of the two species remained substantially separate.

It would appear that some degree of hybridization in *Cassia* is widespread. The actual hybrid nature of these plants will, of course, need to be demonstrated more convincingly by their actual production and by cytological methods. However, their physical placement and number of intermediate characters is very suggestive of a hybrid origin, with ecological selection operating to maintain some degree of uniformity amongst the populations making up the group of species.

V. Acknowledgments

Acknowledgments are due to Mr. G. M. E. Mayo, without whose help and enthusiasm the transect would never have been done, and to several colleagues for their helpful discussions.

* Dobzhansky, Th. (1953).—Natural hybrids of two species of *Arctostaphylos* in the Yosemite region of California. *Heredity* **7** (1): 73-9.

A HYBRID SWARM IN CASSIA

Specimens of the principal *Cassias* discussed. 1, *C. artemisioides*; 2, *C. artemisioides*, a possible backcross plant with woolly tomentum; 3, a suspected hybrid plant; 4, *C. desolata* var. *involucrata*.

THE POLLEN MORPHOLOGY OF *NOTHOFAGUS* BL. SUBSECTION BIPARTITAE STEEN.

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Summary

The pollen morphology of *Nothofagus* Bl. subsection Bipartitae Steen. has been described.

Pollen descriptions of 12 of the New Guinea species and three of the New Caledonian species have been given.

The usefulness of pollen morphology in species determination within the subsection Bipartitae has been considered.

I. Introduction

This study was undertaken at the request of Professor C. G. G. J. van Steenis, in order to determine whether pollen morphology would lend support to the specific determinations made by him in his recent work on the New Guinea beeches (1952, 1953). In this work the large number of 16 species of *Nothofagus* Bl. was distinguished, somewhat hesitatingly, but at the same time the belief was expressed that even when more ample material was available the number of species would not be reduced below 10.

Some doubt still exists regarding the assignment of the New Guinea and New Caledonian beeches to *Nothofagus*. Baumann-Bodenheim (1953) has preferred to regard the New Caledonian forms as generically distinct and has retained the name *Trisyngyne*, originally given by Baillon (1873) to specimens from New Caledonia, whose affinity with the Fagaceae has only recently been determined.

van Steenis (1953, 1954), on the other hand, has brought forward evidence in favour of the inclusion of both series in *Nothofagus*, and has suggested that they be grouped together in a distinct subsection, the Bipartitae.

Langdon (1947), on morphological grounds, has given support to the grouping of the New Guinea species in a distinct subsection of *Nothofagus*.

On the evidence of wood anatomy Dadswell and Ingle (1954) also support this grouping. More recently one of these authors has suggested in a personal communication, on the same grounds, that three of the New Caledonian species (*N. aequilateralis* (Baum.-Bod.), *N. balansae* (Bail.) Steen., and *N. discordea* (Baum.-Bod.)) also belong to this group, being almost indistinguishable in this respect from the New Guinea species.

The pollen morphology of the subsection Bipartitae, whilst distinct from that of the temperate species of *Nothofagus*, is comformable with the systematic placing suggested by van Steenis (1954) for both the New Guinea and New Caledonian

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species. For this reason we propose to adopt the classification put forward by van Steenis, and to treat the New Caledonian species as representatives of *Nothofagus* subsection Bipartitae rather than as members of a separate genus.

II. Pollen Types of Nothofagus

The pollen grains of the various species of *Nothofagus* are basically similar and, as Cranwell (1939) has shown, are in general agreement with those of other anemophilous genera of the Fagaceae.

The grains are small, medium, or large, flattened, with 3-9 (usually 5-7) meridionally elongated pores* equally spaced around the equator of the grain. The exine is spinuliferous.

Three morphological types or pollen groups can be distinguished. Two of these, namely the *menziesii* and *fusca* types have already been treated in detail by Cranwell (1939), the third, which forms the subject of the present paper and which it is herewith suggested should be known as the *brassi* type, characterizes the subsection Bipartitae, the type species of which is *N. brassi* Steen.

The *menziesii* type (Cranwell 1939; Cookson 1946; Couper 1953) is characterized by its large size (equatorial diameter *c.* 40-60 μ), extremely thin exine, and inconspicuous pores or fissure-points around the equator which, when the grains are ruptured, appear as "gaping unrimmed furrows of varying lengths". This type occurs in *N. menziesii* (Hook. f.) Oerst. (New Zealand), *N. cunninghamii* (Hook. f.) Oerst. (Australia and Tasmania), *N. moorei* (F. Muell.) Krasser (Australia), and *N. obliqua* (Mirb.) Oerst. (South America).†

The *fusca* type (Cranwell 1939; Cookson 1947; Couper 1953) is characterized by its medium size, convex polar surfaces, and firm exine which is distinctly thickened around the pores. Species with this type of pollen are *N. fusca* (Hook. f.) Oerst., *N. truncata* (Col.) Cockayne, *N. solandri* (Hook. f.) Oerst., and *N. cliffortioides* (Hook. f.) Oerst. (New Zealand); *N. pumilio* (Poepp. & Endl.) Krasser, *N. dombeyi* (Mirb.) Oerst., *N. antarctica* (Forst.) Oerst., *N. betuloides* (Mirb.) Oerst., and *N. alessandri* Espinosa (South America); and *N. gunnii* (Hook. f.) Oerst. (Australia).

The *brassi* type (Cookson 1952; Erdtman 1954) has an angular amb and a firm exine which, unlike that of the *fusca* type, is unthickened around the pores. All the species with this type of pollen belong to the subsection Bipartitae and occur only in New Guinea and New Caledonia.

III. Pollen Descriptions of Nothofagus (Subsection Bipartitae)

The pollen preparations upon which the following descriptions have been based were made according to the Erdtman acetolysis schedule (Erdtman 1943), the acetolysed grains being mounted either in uncoloured or Safranine glycerine jelly.

* The apertures, although $\pm$ colpoid, are referred to as pores on account of their rounded ends (Faegri and Iversen 1950, p. 20).

† *Note added in Proof.*—This type also occurs in the South American species *N. procera* (Poepp. & Endl.) Oerst. (see Auer, Salmi, and Salminen 1955).

Anthers of 12 of the New Guinea species and three of the five New Caledonian species were treated. Unfortunately, male flowers are seldom abundant in herbarium collections of *Nothofagus*, and this has been the condition of the majority of the New Guinea and New Caledonian sheets. Most of the material available to us has consisted of only a few anthers, and thus has been inadequate for accurate statistical details. The percentage pore-frequencies included in the individual descriptions are, therefore, to be regarded as merely approximate.

Diagnosis.—Pollen grains of the *brassi* type are small to medium, isopolar to slightly subisopolar*, peroblate to suboblate, polygonal in polar view with straight to slightly concave sides and 3-8 (usually 4-7), longitudinally elongated, clearly rimmed pores at the angles. The exine, which is about 0·7-1·6 μ thick, is not thickened around the pores; it is covered with a variable number of more or less prominent spinules,† which are usually smaller and more widely scattered towards the equator and always absent from the annular region surrounding each pore; the sexine is thinner than the nexine.

(*a*) *New Guinea Species*

1. *Nothofagus recurva* Steen. Kostermans 2321 ex Leiden 953133

Figs. 1*A*, 1*B*; Plate 1, Figs. 1, 2

Polar diameter range 11-13, av. 11·5 μ; equatorial diameter range 21-29, av. 26 μ; peroblate; pores 4-7, mainly 5 and 6, majority 6 (4, 1 per cent.; 5, 45 per cent.; 6, 53 per cent.; 7, 1 per cent.). Exine *c.* 1·1 μ, almost smooth; spinules small, less than 0·5 μ long, 24-35 per 100 sq. μ of polar surface.

1(*a*). *Nothofagus recurva* var. *microphylla* Steen. Kanehira and Hatusima 14052 ex Leiden

Figs. 2*A*, 2*B*; Plate 1, Figs. 3, 4

Polar diameter range 11-13, av. 12 μ; equatorial diameter range 20-25, av. 23 μ; oblate; pores 4-6, majority 5 (4, 14 per cent.; 5, 84 per cent.; 6, 2 per cent.). Exine *c.* 1·3 μ; spinules rather larger than those of *N. recurva*, *c.* 0·75 μ long, 30-41 per 100 sq. μ.

2. *Nothofagus starkenborghi* Steen. Brass 11369 ex Leiden.

Figs. 3*A*, 3*B*; Plate 1, Figs. 5, 6

Polar diameter range 13-15, av. 14 μ; equatorial diameter range 24-30; av. 26 μ; oblate; pores 4-7, mainly 5 and 6, majority 5 (4, 1 per cent.; 5, 50 per cent.; 6, 49 per cent.). Exine *c.* 1·2 μ; spinules less than 0·5 μ long, 42-55 per 100 sq. μ.

3. *Nothofagus brassi* Steen. Brass and Versteegh 11115 ex Arn. Arb.

Figs. 4*A*, 4*B*; Plate 1, Figs. 7, 8

Polar diameter range 11-16, av. 14 μ; equatorial diameter range 27-32, av. 29; oblate; pores 5-7, majority 6 (5, 8 per cent.; 6, 77 per cent.; 7, 15 per cent.). Exine *c.* 1·1 μ; spinules about 0·5 μ long, 40-50 per 100 sq. μ.

* Sometimes there are more spinules per unit area on one pole than on the other.

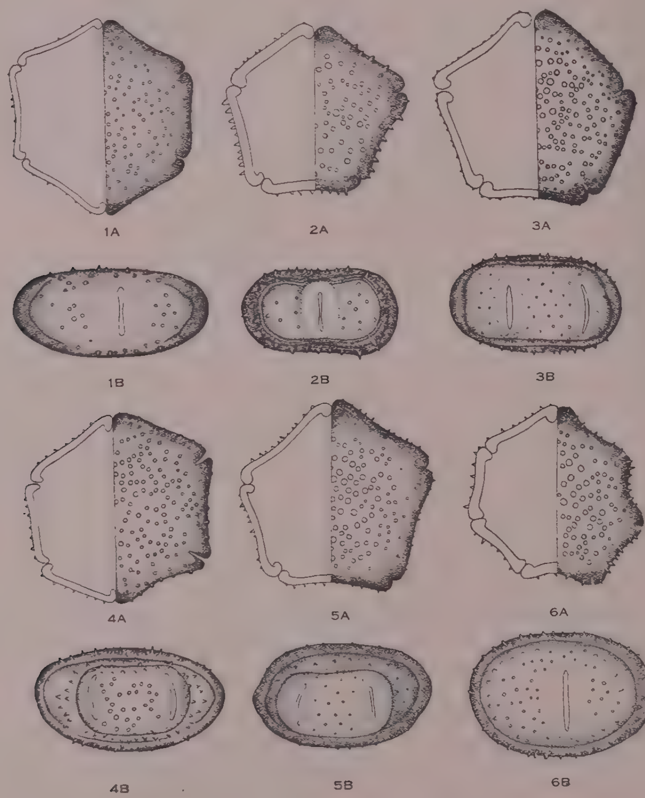
† A tendency towards a spiral arrangement has been noticed.

4. *Nothofagus pullei* Steen.

(i) Clemens 7510 ex Leiden

Figs. 6*A*, 6*B*; Plate 1, Figs. 10, 11

Polar diameter range 11-14, av. 12 μ: equatorial diameter range 23-25, av. 24 μ: peroblate; pores 5-7, mainly 6 and 7 (5, 1 per cent.: 6, 52 per cent.: 7, 47 per cent.). Exine *c.* 1·1 μ; spinules *c.* 0·75 μ long, 35-53 per 100 sq. μ.



Figs. 1-6.—Camera lucida drawings of pollen grains in polar (*A*) and equatorial (*B*) view. × 1000. Fig. 1.—*Nothofagus recurva.* Fig. 2.—*N. recurva* var. *microphylla.* Fig. 3.—*N. starkenborghi.* Fig. 4.—*N. brassi.* Fig. 5.—*N. pullei*, Pulle 909. Fig. 6.—*N. pullei*, Clemens 7510.

(ii) Pulle 909. ex Leiden 951297 (Type)

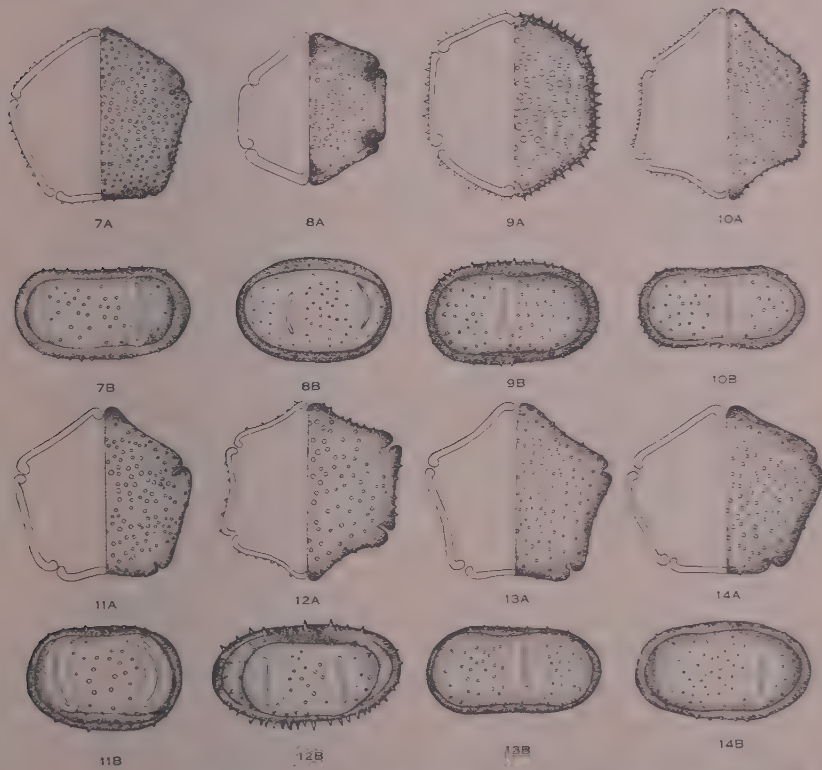
Figs. 5*A*, 5*B*; Plate 1, Fig. 9

Polar diameter range 9-12, av. 11 μ; equatorial diameter range 20-27, av. 24 μ; peroblate; pores 4-6, mainly 5 and 6, majority 5 (4, 1 per cent.; 5, 65 per cent.; 6, 34 per cent.). Exine *c.* 1·0 μ; spinules *c.* 0·75 long, 40-53 per 100 sq. μ.

5. *Nothofagus resinosa* Steen. Brass 10479 ex Leiden

Figs. 7*A*, 7*B*; Plate 1, Figs. 12, 13

Polar diameter range 11-12, av. 11 μ; equatorial diameter range 20-25, av. 23 μ; peroblate; pores 3-6, mostly 4 and 5, majority 5 (3, 2 per cent.; 4, 18 per cent.; 5, 75 per cent.; 6, 5 per cent.). Exine *c.* 1·2 μ, almost smooth under oil immersion; spinules small, short and numerous, 65-76 per 100 sq. μ.



Figs. 7-14.—Camera lucida drawings of pollen grains in polar (*A*) and equatorial (*B*) view. × 1000. Fig. 7.—*Nothofagus resinosa*. Fig. 8.—*N. carri*. Fig. 9.—*N. bernhardi*. Fig. 10.—*N. grandis*. Fig. 11.—*N. decipiens*. Fig. 12.—*N. rubra*. Fig. 13.—*N. eymae*. Fig. 14.—*N. dura*.

6. *Nothofagus carri* Steen.

(i) Carr 15028 (Type)

Figs. 8*A*, 8*B*; Plate 1, Fig. 14

Polar diameter range 12-15, av. 14 μ; equatorial diameter range 16-22, av. 19 μ; oblate; pores 4-6, majority 5 (4, 14 per cent.; 5, 78 per cent.; 6, 8 per cent.). Exine *c.* 1·6 μ, smooth under oil immersion; spinules small, very short, 69-78 per sq. μ.

(ii) Carr 15076 ex Leiden

Polar diameter range 12-16, av. 15 μ; equatorial diameter range 19-23, av. 20 μ; oblate; pores 4-6, majority 5 (4, 22 per cent.; 5, 75 per cent.; 6, 3 per cent.). Exine *c.* 1·5 μ, smooth; spinules very short, 56-65 per sq. μ.

(iii) Carr 13766 ex Leiden 936248

Plate 1, Fig. 15

The pollen of this specimen differs from that of Carr 15028 and 15076 in the higher proportion of 6-pored (approx. 42 per cent.) and apparent absence of 4-pored grains.

7. *Nothofagus bernhardi* Steen. Brass 12453 ex Leiden

Figs. 9*A*, 9*B*; Plate 1, Figs. 16, 17, 18

Polar diameter range 12-15, av. 13 μ; equatorial diameter range 18-27, av. 23 μ; oblate; pores 4-6, mainly 5 and 6, majority 6 (4, 3 per cent.; 5, 44 per cent.; 6, 53 per cent.). Exine *c.* 1 μ; spinules prominent, *c.* 1 μ long, 50-65 per 100 sq. μ.

8. *Nothofagus grandis* Steen. Coll. Schindler, Aiyura

Figs. 10*A*, 10*B*; Plate 1, Figs. 19, 20

Polar diameter range 11-14, av. 13 μ; equatorial diameter range 20-27, av. 23 μ; oblate; pores 5-7, majority 6 (5, 33 per cent.; 6, 65 per cent.; 7, 2 per cent.). Exine *c.* 1·2 μ; spinules *c.* 0·7 μ long, 52-68 per 100 sq. μ.

9. *Nothofagus decipiens* Steen. Brass 12675 ex Leiden and Arn. Arb.

Figs. 11*A*, 11*B*; Plate 1, Figs. 21, 22

Polar diameter range 10-14, av. 12 μ; equatorial diameter range 23-29, av. 25 μ; oblate; pores 4-7, majority 5 (4, 6 per cent.; 5, 88 per cent.; 6, 5 per cent.; 7, 1 per cent.). Exine *c.* 1 μ, smooth; spinules short, less than 0·5 μ, 45-55 per 100 sq. μ.

10. *Nothofagus rubra* Steen. Brass and Versteegh 11977a ex Leiden, 99441

Figs. 12*A*, 12*B*; Plate 1, Figs. 23, 24

Polar diameter range 11-14, av. 13 μ; equatorial diameter range 19-26, av. 23 μ; oblate; pores 5-7, majority 6 (5, 5 per cent.; 6, 81 per cent.; 7, 14 per cent.). Exine *c.* 0·70 μ; spinules *c.* 0·6 μ long, 27-35 per 100 sq. μ.

11. *Nothofagus eymae* Steen. Eyma 4800 (Type) ex Leiden 951296

Figs. 13*A*, 13*B*; Plate 1, Figs. 25, 26

Polar diameter range 10-12, av. 11 μ; equatorial diameter range 23-29, av. 26 μ; peroblate; pores 4-7, mainly 5 and 6, majority 6 (4, 0·5 per cent.; 5, 44 per cent.; 6, 55 per cent.; 7, 0·5 per cent.). Exine *c.* 0·75 μ; spinules short, widely variable in number, 30-70 per 100 sq. μ.

12. *Nothofagus dura* Steen. Brass and Versteegh 10443 ex Leiden 94941

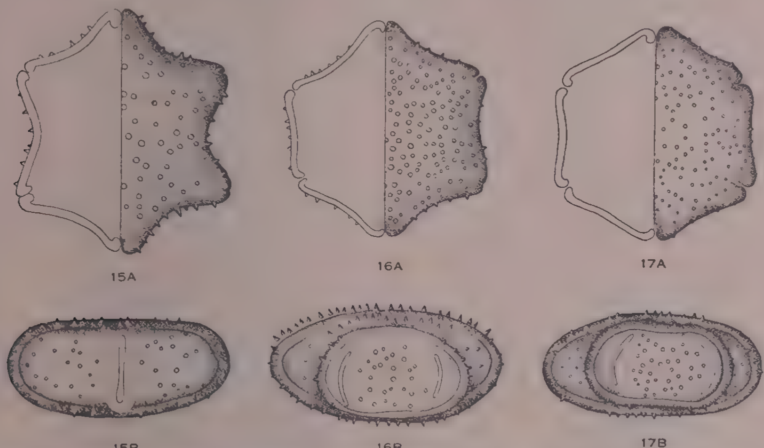
Figs. 14*A*, 14*B*; Plate 1, Figs. 27, 28

Polar diameter range 9-11, av. 10 μ; equatorial diameter range 18-25, av. 22 μ; peroblate; pores 3-5, mainly 4 and 5 (3, 1 per cent.; 4, 49 per cent.; 5, 50 per cent.). Exine *c.* 0·83 μ, almost smooth; spinules short, less than 0·5 μ, 37-47 per 100 sq. μ.

(*b*) *New Caledonian Species*

13. *Nothofagus balansae* (Bail.) Steen. (Type) Balansa 1377 ex Paris Herb.
Figs. 15*A*, 15*B*; Plate 1, Figs. 29, 30

Polar diameter range 11-14, av. 13 μ; equatorial diameter range 25-36, av. 28 μ; peroblate; pores 5-7, majority 6 (5, 7 per cent.; 6, 79 per cent.; 7, 14 per cent.). Exine *c.* 1·2 μ; spinules *c.* 1 μ, sparse, 10-23 per 100 sq. μ.



Figs. 15-17.- Camera lucida drawings of pollen grains in polar (*A*) and equatorial (*B*) view. × 1000. Fig. 15.—*Nothofagus balansae*. Fig. 16.—*N. baumanniae*. Fig. 17.—*N. codonandra*.

14. *Nothofagus baumanniae* (Baum.-Bod.) Steen. ex Baumann-Bodenheim No. 15626
Figs. 16*A*, 16*B*; Plate 1, Figs. 31, 32

Polar diameter range 14-15, av. 15 μ; equatorial diameter range 27-34, av. 32 μ; peroblate; pores 5-7, majority 6 (5, 25 per cent.; 6, 72 per cent.; 7, 3 per cent.). Exine *c.* 0·83 μ; spinules less than 0·5 μ long, 29-40 per 100 sq. μ.

15. *Nothofagus codonandra* (Baum.-Bod.) Steen. No. 3557 ex Herb. Mus. Paris
Figs. 17*A*, 17*B*; Plate 1, Figs. 33, 34

Polar diameter range 11-15, av. 13 μ; equatorial diameter range 23-34, av. 29 μ; peroblate; pores 5-8, mainly 6 and 7, majority 6 (5, 1 per cent.; 6, 55 per cent.; 7, 43 per cent.; 8, 1 per cent.). Exine *c.* 1 μ; spinules short, 26-37 per 100 sq. μ.

IV. Discussion

In contrast to the position in the two large temperate subsections of *Nothofagus*, the Antarcticae and Quadripartitae of van Steenis, in which both the *menziesii* and *fusca* pollen types occur, the pollen of the subsection Bipartitae is uniform throughout. Slight differences between the pollen grains of the species examined have been observed, but these are sometimes difficult to appreciate even with high magnifications. A few of the types are well characterized, others would be difficult, if not impossible, to identify with any degree of certainty in a pollen mixture involving a number of species.

The most useful distinguishing characters appear to be the size of the grains, the thickness of the exine, and the size and number of the exinous spinules, although even with these characters a certain amount of overlap occurs.

Percentage pore-frequency and pore-majority values seem to be less reliable, since in a few examples they can be shown to vary with the locality in which the species was growing. For example, anthers of *Nothofagus pullei* (Pulle 909) from western New Guinea gave pollen grains with a pore-range of from 4 to 6, and a majority of 5, whereas in material of the same species from north-eastern New Guinea (Clemens 7510) the range was from 5 to 7 with 6-pored grains predominating. A somewhat similar situation was met with in the material of *N. carri*, which included anthers from three separate collections. Two of these, Carr 15028 (Type) and Carr 15076 (van Steenis 1953, p. 359) yielded pollen grains with a pore range of from 4 to 6, the majority being 5-pored; the third, Carr 13766, whilst still showing a majority of 5-pored grains, gave a pore range of from 5 to 7. A similar inconstancy was recorded by Cookson (1947) for *N. gunnii*, the Tasmanian representative of the *fusca* pollen group.

Two series within the section Bipartitae have been suggested by van Steenis (1953), the Triflorae and the Uniflorae. The series Triflorae comprises the five New Caledonian species, pollen of three of which (*N. baumanniae*, *N. balansae*, and *N. codonandra*) have been described herein, and the New Guinea species *N. perryi* (male flowers not available), *N. recurva*, *N. brassi*, and *N. starkenborghi*. When considered as a whole the pollen grains of this series can be said to be larger and to include a greater number of six-pored examples than those of the Uniflorae—*N. baumanniae* has the largest grains of the whole subsection, with those of *N. codonandra*, *N. balansae*, and *N. brassi* in close approximation to them. The pollen grains of *N. balansae* can be readily distinguished from those of *N. codonandra* and *N. baumanniae* as well as from all the New Guinea pollen types, by their small number of polar spinules (10-23 per 100 sq. μ). The grains of *N. brassi*, which are the largest of the New Guinea species, are practically indistinguishable from those of *N. codonandra* and *N. baumanniae*, whilst they only differ from those of the remaining members of the Triflorae, *N. recurva* and *N. starkenborghi*, in the smaller number of spinules of the former and the slightly thicker exine of the latter. On pollen morphological grounds therefore the New Caledonian and New Guinea species of the series Triflorae seem to be closely related.

At this point attention may be drawn to the divergence of the pollen grains of *N. recurva* var. *microphylla* from those of *N. recurva*. The grains of the variety are smaller and have thicker exines, longer spinules, and a different pore number than those of the type.

Of the series Uniflorae, which comprises the majority of the New Guinea species, *N. carri* and *N. bernhardi* have the most distinctive pollen grains. Those of *N. carri*, besides being the smallest of the known living species of *Nothofagus*, with an average equatorial diameter of about 20 μ, can be distinguished from those of all other members of the Bipartitae by the relatively thick exine and, owing to the shortness of the spinules, its smooth appearance in optical section. *N. bernhardi*, on the

contrary, possesses the most spiny pollen type, the spinules, about 1 μ long, projecting well beyond the surface of the exine in polar views.

The pollen grains of *N. resinosa*, although agreeing with those of *N. carri* in having a large number of exinous spinules (65-76 per 100 sq. μ), can be distinguished from them by their larger size, thinner exines, and longer spinules.

N. dura and *N. decipiens* have pollen grains that are practically identical with one another. Both types differ from the remaining members of the series (*N. rubra*, *N. eymae*, *N. pullei*, and *N. grandis*) in having almost smooth exines. The grains of *N. decipiens* are somewhat larger and have a greater number of spinules than those of *N. dura*, but it is doubtful whether these differences are sufficiently well defined to distinguish between them.

The pollen grains of *N. rubra*, *N. eymae*, *N. pullei*, and *N. grandis* are all very much alike, and again it is improbable that the minute differences between them would be sufficient for taxonomic purposes.

In conclusion, the occurrence of pollen of the *brassi* type in the Tertiary deposits of Australia (Cookson 1946, 1952, 1954) and New Zealand (Couper 1953) should be mentioned. Couper has shown that pollen grains of this type (his *cranwellae* group)* antedated those of the *menziesii* and *fusca* types, their earliest appearance being in the Lower Cretaceous (Paparoa beds, Te Punga (1947)). The position as far as Australia is concerned is not nearly so clearly defined. Up to the present pollen grains of *Nothofagus* have not been found in rocks older than Early Tertiary. Pollen grains of the *brassi* type have been observed in Pliocene deposits in Papua, New Guinea.

Finally it has been interesting to observe the frequent occurrence in a deposit of more than one variety of the *brassi* pollen type, occasionally as many as four or five in a rich deposit. This fact is in conformity with the tendency shown by the living representatives of the subsection Bipartitae, of which, in some areas of New Guinea, several species are to be found living together.

V. Acknowledgments

Most of the New Guinea material for the present investigation was generously provided by Professor van Steenis from the Leiden collection, but important additions were kindly made available by Dr. Kobuski, Arnold Arboretum, and Mr. J. S. Womersley, Forest Department, Lae.

Thanks to the liberal cooperation of Dr. M. G. Baumann-Bodenheim, Zurich, pollen of three of the five fagaceous species from New Caledonia was procured, with the result that direct comparisons with the pollen grains of New Guinea species could be included here.

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*It is suggested that fossil pollen grains referable to *Nothofagus* subsection Bipartitae should collectively be referred to as the *brassi* type so as to bring them into line with fossil representatives of the *menziesii* and *fusca* types respectively.

VI. References

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Explanation of Plate 1

All the photographs are from untouched negatives. The figures are of acetolysed pollen grains, magnified 750 times.

Figs. 1, 2.—*Nothofagus recurva.*
Figs, 3, 4.—*N. recurva* var. *microphylla.*
Figs. 5, 6.—*N. starkenborghi.*
Figs. 7, 8.—*N. brassi.*
Fig. 9.—*N. pullei,* Pulle 909.
Figs. 10, 11.—*N. pullei,* Clemens 7510.
Figs. 12, 13.—*N. resinosa.*
Fig. 14.—*N. carri,* No. 15028.
Fig. 15.—*N. carri,* No. 13766.
Figs. 16-18.—*N. bernhardi.*
Figs. 19, 20.—*N. grandis.*
Figs. 21, 22.—*N. decipiens.*
Figs. 23, 24.—*N. rubra.*
Figs. 25, 26.—*N. eymae.*
Figs. 27, 28.—*N. dura.*
Figs. 29, 30.—*N. balansae.*
Figs. 31, 32.—*N. baumanniae.*
Figs. 33, 34.—*N. codonandra.*

POLLEN MORPHOLOGY OF NOTHOFAGUS